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THE THIRD ANOLIS NEWSLETTER

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DEDICATED TO THE MEMORY OF

THOMAS PRESTON WEBSTER

WHO DIED IN AN AUTOMOBILE ACCIDENT NOVEMBER 9, 1975

Note to contributors and subscribers

As the delay since the Second Anolis Newsletter has made very obvious, this is an irregular periodical with no schedule except that which the time and the opportunity of the Editor permit. Originating, as the preface to the Second Newsletter explained, as an in-house memorandum of information, it now aspires to wider currency. It remains, however, primarily informational: news (and sometimes comment) about current and proposed work on biological and evolutionary aspects of the genus Anolis.

Even with this third installment it has not achieved uniformity either of style or content. The Editor is not unhappy about this; he is not sure that uniformity is necessary or desirable. The reports by individual workers on Anolis should reflect the interests, methods and even manner of the individual concerned. The Editor intervenes only to make sure that what is said is relatively intelligible to most readers and interesting to many. There is a general request that nothing said herein shall be quoted without the authors' express permission. The Editor does not believe in this requirement himself, not being of the opinion that everything more formally published has necessarily more validity or permanence than what is stated here. The Editor would in fact prefer a certain looseness of style and freedom of expression but he does not overrule the authors in this regard.

Line cuts and other xeroxable figures are encouraged. Length is not a primary consideration, but it is not intended that formal or fully documented papers be accepted here. Rather the Editor believes that this is an appropriate place for first exposure to the general eye of observations, suggestions, opinions and comments that will not be published elsewhere in the near future and perhaps not at all. An important new contribution may be summarized by its author for the purpose of attracting comment (e.g. Shochat and Dessauer herein) but the Editor would discourage mere notices of papers that will soon appear. Reports of work underway or newly embarked on or of a publication that will be long delayed are very appropriate.

As with other Newsletters, at the wish of the contributor references may be inserted in the text or provided as a bibliography. If the references are in the text only, please provide author, date, journal volume and pagination. If there is a bibliography, the citation should be given with the full title.

The Editor will not abstract manuscripts as he did in the Second Newsletter. He finds that this task delays too much the publication via the Newsletter of the reports he does receive. As a substitute he is instituting a list of Anolis publications that he is aware of or has received. The current list records papers of 1973 to the end of 1976.

Contributors receive the Newsletter, and libraries may request free copies. All others must pay the cost of reproduction and of mailing.

An anecdote

It was while walking along a hedge row in the Dominican Republic, listening to a complaint that I and some of my co-workers did not frame hypotheses every day while in the field, that I invented (or recognized) the PRINCIPLE OF UNSYMPATHETIC MAGIC. This states that, if one arrives at any firm and vivid conviction about matters of fact or theory in the field, the NEXT observation will provide a contradiction.

The principle is easily confirmed by any field worker. Note, however, that NATURE IS NOT DECEIVED. No opinion merely pretended to, i.e. not held with fierce conviction, will be responded to by a conclusive observation. The MALICE OF NATURE prohibits the PRINCIPLE OF UNSYMPATHETIC MAGIC from being a source of satisfaction to the field worker.

Acknowledgment

The Harvard reports herein were supported in whole or in part by National Science Foundation grant NB-37731X and previous grants to E. E. Williams.

ROBIN ANDREWS (Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061) reports on studies of Anolis limifrons in Panama.

A. S. Rand and I have been censusing A. limifrons on Barro Colorado Island (BCI) since November, 1971. This study was initiated to document both seasonal and long-term changes in demographic characteristics of this small shrub-ground anole. Seasonal changes in composition and density of the population result from its annual turnover and variation in recruitment throughout the year. Reproduction is low during the dry season. Eggs laid early in the wet season hatch in June and recruitment continues throughout the rest of the wet season. Population density is the greatest late in the wet season when many juveniles and recently matured adults are present. The long-term changes in population density that we have observed are shown by the census data from the latter part of the wet season (Table 1). Population densities were the greatest when the study began in 1971 with 94 adults and a total of at least 130 individuals if juveniles were included. Population density declined in 1972 and was very low during the next three years. The results of the 1976 census indicate that population density may be increasing.

Our studies on the demography of A. limifrons have the ultimate goal of understanding why the population fluctuates so markedly in size. Of the major kinds of factors that could be involved, food availability seems the least likely. One line of evidence is that fluctuations in anole abundance are independent of the fluctuations in arthropod abundance as measured by light trap collections. Moreover, juvenile growth rates are very similar in years of high and low anole abundance. Predation or weather, or some combination of the two, are more likely factors to affect population size. Previously, we had assumed that most mortality was due to birds, snakes and large predaceous arthropods such as spiders and mantids. Recently, however, A. S. Rand and S. Guerrero have begun to study some blood and liver parasites that are potential sources of mortality (see Rand's report for details). O. J. Sexton has suggested that weather could affect population density through egg mortality if the number of eggs laid and their survival depend on the length and severity of the dry period.

My principal objective in the A. limifrons study at present is the construction of a demographic model that can be used to simulate the effect of changes in population class composition, mortality, and fecundity. I spent this spring in Panama collecting data not available from census records that is necessary for the completion of this model. I determined the fecundity of full grown and sub-adult females that had been fed quantities of food similar to those eaten by females in the field. Almost half of the full-grown females in my cage population (N = 17) had malaria parasites in their blood. These individuals did not differ in rate of egg production from non-parasitized individuals. Low level (0.1-4.0% of red blood cells parasitized) infections such as these apparently do not affect fecundity. I also determined mortality rates of A. limifrons eggs that I "laid" in the field. Although these eggs have not yet been followed to hatching, initial loss rates suggest that about half will survive the incubation period. Laboratory studies are also in progress to determine the survivorship of eggs on soils of different water

availabilities. This information in conjunction with data that is available on seasonal changes in soil water near our study areas will tell us the ability of eggs to survive dry periods.

One of three seasonal life tables that I have determined for A. limifrons is shown in Table 2. It gives fecundity and survivorship values for the early part of the wet season (May-August). The other two live tables differ primarily in having lower survivorship of both juveniles and adults during the latter part of the wet season (Sept.-Dec.) and in very low egg survivorship during the dry season (Jan.-April).

This demographic information is incorporated in a Leslie Matrix model The effect of seasonality on population dynamics is handled in the model by switching between three matrices with survivorship and fecundity values appropriate for the early wet season, the late wet season, and the dry season. The model simulates the changes in class composition and density of the population through its yearly cycle very well. It also indicates that the yearly cycle of egg production may be more complex than had been anticipated. The simulated number of eggs laid is low during the dry season, rises rapidly shortly after the rains begin, and then slowly declines until October when numbers rise rapidly again. Egg production declines during the wet season as the adult females that survived through the dry season gradually die off. The eggs laid in May produce mature females in October, thus the second peak in eggs laid. Further work with this model will be conducted this summer to answer such questions as: is there an optimal time for females to lay eggs in terms of long-term contribution to subsequent generations? and, what effect does variation in length of the dry season have on population dynamics?

Table 1. Population size of Anolis limifrons on the 830 m^2 study area on BCI. Adult population size was estimated by a regression method or with the Petersen Index. The numbers of juveniles are represented by the total numbers captured during the census period because high turnover of this class invalidates population size estimators.

	Late wet season
	No. adults (no. juveniles)
1971	94 (43)
1972	44 (27), 29 (27)
1973	26 (14)
1974	23 (13)
1975	-
1976	42 (22)

Table 2. Early wet season life table for A. limifrons. S_x is the proportion of females that survive each 28 day time interval and m_x is the number of female eggs laid during the same interval.

Age (days)	Class	S_x	m_x
0	egg	.67	0
28	egg	.67	0
56	19 mm SVL	.6	0
84	25	.6	0
112	30	.6	0
140	35	.8	0
168	40	.8	1
196	42	.8	1.2
224	44-49	.9	2.3
252	44-49	.9	2.3

STEPHEN C. AYALA (Universidad del Valle, Cali, Colombia) has become involved with the Anolis group via his continued interest in malaria in reptiles. A binational NSF proposal (Ayala and Rand) funds active investigations on the populational effects of malaria in Anolis limifrons in Panama. Work there is being done by Rand, Stella Guerrero and Robin Andrews. A parallel Colombian grant (Ayala) funds work in Colombia by Ayala and his Cali colleagues, Humberto Carvajal, Helen Chin, Bob Godshalk, Carlos Galvis, Fernando Castro, with the assistance of Jorge Hernandez, Federico Medem and William Duellman.

Ayala's observations that are the background of this intensive endeavor are reported by him here (Rand and Guerrero report some of the preliminary results separately below).

The impact of malaria infections on morbidity or mortality of reptile populations has never been assessed. Clinically ill reptiles with natural infections have been reported and there are descriptions of extensive pathological effects, becoming extreme in acutely ill animals. The same can be said for mammal populations (man excepted), and the situation with birds is only slightly better known. Information must be largely drawn from caged "laboratory populations" since wild populations have been so very little studied. If human morbidity criteria are applied to infected wildlife, including lizards, malaria must be considered a widespread, severe and debilitating infection.

Malaria is probably more common in lizards than in any other wild vertebrate populations. Although still very little surveyed, several investigators have commented that there must be some mortality, especially among young animals. There are several slow-reproducing Plasmodium species, like P. carinii (syn. rhadinurum) of I. iguana, that only cause sickness in otherwise debilitated lizards. I found one Iguana harboring both tuberculosis and an intense P. rhadinurum infection. This is the only time I've seen an iguana potentially incapacitated by malaria. There is an intermediate group of malarias that act like P. vivax or P. malariae in man, where a certain amount of debilitation must almost always occur in any individual infection (the P. floridensi and P. tropiduri groups of Neotropical lizards including anoles). At the very least, these erythrocyte-destroying infections cause marked anemia and require compensatory erythropoiesis lasting several weeks. In an emergency, the lizard may go clear back to embryo-like stem-cell sources to produce the necessary erythrocytes as quickly as possible.

The most severely affected lizards probably retreat to cool sites and remain inactive (lowering their oxygen needs). They are lethargic in the hand and may die soon after capture. I suppose that such animals are usually missed by normal collecting methods and many probably die unannounced in their hiding places.

Plasmodium species sometimes undergo severe seasonal relapses - known as "spring relapses" in temperate zones, although whether the key association is with "spring," seasonal increases in transmitting insect abundance, or hormonal changes associated with host reproductive periods is not known. The P. mexicanum-group species of Sceloporus lizards are potentially quite pathogenic.

They reproduce in endothelial cells lining the capillaries of the brain, as well as within the erythrocytes. During the April-June "spring relapse," there is no doubt of widespread extensive mortality especially in yearlings emerging from their first winter hibernation.

Most lizards probably remain infected for the remainder of their life once they acquire malaria. This is especially the case with the shorter life-span species like anoles. Thus, there is a continuously increasing prevalence concurrent with increasing age and older animals are more likely to carry the parasite(s).

However, lizards probably survive the acute phase of the infection in most cases, and most of the observed infections are chronic. Severe, incapacitating or potentially fatal disease probably occurs only during the first month or two following initial infection, or during periods of relapse that may (or may not?) be synchronized with the host reproductive seasons. Infections are usually severe in young, newly-infected lizards (but not so in newly-infected hatching Sceloporus in October in California, when both hatchling and parasite are preparing for winter). It seems that with anoles, a significant proportion of the infections are acquired around the time of sexual maturity or soon thereafter. There often seems to be a slightly higher prevalence in males, but the validity or significance of this has not yet been discovered.

MALARIA SPECIES REPORTED FROM NATURALLY INFECTED ANOLES

1) Plasmodium azurophilum Telford 1975 (a rather unique protozoan; nearest relatives unknown): Anolis cybotes Haiti; A. grahami Jamaica; A. krugi Puerto Rico; A. lineatopus Jamaica.

2) Plasmodium balli Telford 1969 (a striking parasite that causes marked distortion of the erythrocyte nucleus; probably widely dispersed in South and Central American anoles): A. chloris Colombia; A. fuscoauratus Peru, Colombia; A. limifrons Panama; A. lionotus Panama; A. poecilopus Panama; A. vittigerus W. Colombia; A. sp. Brasil.

3) Plasmodium colombiense Ayala & Spain 1975: A. auratus W. Colombia, Venezuela.

4) Plasmodium floridense Thompson & Huff 1944 (scarcely distinguishable from P. tropiduri of Tropidurus spp from Brasil and northern South America; in Florida and Georgia it also infects Sceloporus undulatus, producing much more severe malaria than it does in the anoles): A. biporcatus Panama; A. carolinensis Florida, Georgia; A. concolor San Andres Island; A. conspersus G. Cayman Island; A. cybotes Haiti; A. distichus Haiti; A. frenatus Panama; A. garmani Jamaica; A. grahami Jamaica; A. limifrons Panama; A. lineatopus Jamaica; A. opalinus Jamaica; A. pentaprion Panama; A. pulchellus Puerto Rico; A. sagrei N. Bimini, Bahamas.

5) "Plasmodium minasense" sensu Telford 1974 (probably a yet-to-be-named species): A. capito Panama; A. frenatus Panama; A. limifrons Panama.

6) Plasmodium torrealbae Scorza and Daggett 1957: Anolis sp. Venezuela.

7) Plasmodium "tropiduri" sensu Telford 1974 (probably not the same parasite as P. tropiduri from Tropidurus spp): A. biporcatus Panama; A. frenatus Panama; A. limifrons Panama; A. lionotus Panama; A. pentaprion Panama.

8) Plasmodium utingensis Lainson, Shaw & Landau 1971: A. punctatus Brasil.

9) Plasmodium sp.: A. aequatorialis Ecuador; A. aquaticus Costa Rica; A. biporcatus W. Colombia; A. cupreus Costa Rica; A. eulaemus Colombia; A. frenatus Costa Rica, Panama; A. fuscoauratus Brasil; A. humilis Costa Rica; A. latifrons W. Colombia; A. lemurinus Costa Rica, Belize; A. limifrons Costa Rica; A. lionotus Panama, Costa Rica; A. poecilopus Panama; A. squamulatus? Venezuela; A. tropidonotus Guatemala.

(Recent Ayala references: Plasmodia of reptiles, in PROTOZOA OF MEDICAL AND VETERINARY INTEREST, J. Kreier, ed, Vol. 3, Chap. 6: 267-309, 1977, Academic Press. Checklist, host index and annotated bibliography of the plasmodia of reptiles, J. Protozool., Vol. 24, 1977 (in press).)

DAVID CREWS (Harvard University) continues his work on the reproductive physiology of Anolis and other reptiles. Here is his Anolis report:

I. Hormonal control of male sexual behavior.

Previous experiments have demonstrated that castration abolishes male courtship behavior in Anolis carolinensis, and consequently prevents male courtship facilitation of environmentally-induced ovarian recrudescence in winter dormant females. Androgen replacement therapy (subcutaneous implants of crystalline testosterone propionate, TP), to castrated males restores the normal pattern of male courtship behavior to its preoperative levels and hence facilitates ovarian growth. However, in this and early work (e.g., Noble and Greenberg, 1941, J. Exp. Zool.), the size of the implants (6 mg) was probably unnecessarily large; Mason and Adkins (1976, Horm. Behav.) have reported recently that daily injections of 20 µg of TP will rapidly restore sexual behavior to intact levels in castrated male A. carolinensis. To approximate more closely the physiological levels of androgen in sexually active males, we have initiated a series of hormone replacement studies using 1 cm silastic capsules (I.D. 0.030 in.) containing 6 mm of hormone; control animals receive equivalent amounts of cholesterol. Briefly, intact males are tested in their home cage each day with unfamiliar males and females to determine their level of aggressive and sexual behavior (see Crews, 1975, Herpetologica, for description of these behavior patterns). Males are then castrated and the decline in reproductive behavior monitored; when the castrated male no longer responds to an introduced lizard, a 1 cm silastic capsule is implanted subcutaneously.

Preliminary results indicate that a testosterone capsule of this size will effectively reinstate male reproductive behavior in castrated, sexually inactive males within four days of implantation(Figure 1). Interestingly, assertion behavior appears to be restored first with courtship behavior appearing several days later. Estradiol and dihydrotestosterone alone have no effect on the behavior of castrated males. There does, however, appear to be a synergism between E and DHT, suggesting that central action of E may require developed peripheral tissues(Figure 2).

II. Stimulus control of male copulatory behavior.

Male A. carolinensis exhibit a very stereotyped mating pattern which is characteristic of Anolis lizards in general. Briefly, the male approaches the female, pausing to perform a series of species-typical courtship displays. If the female is receptive, she will stand for the male and arch her neck, allowing the male to take a neck-grip. The male then swings his tail beneath the female's tail, forcing it up and opposing the cloacal openings. The male then everts a hemipenis and intromits (see Figure 2 in Crews, 1973, Physiol. Behav., for a drawing of the copulation posture of A. carolinensis). Since male lizards have two hemipenes, it is possible to tell which hemipenis is intromitted by the angle of deflection of the male's tail; for example, if the male is on the female's left side, the male's tail will be angled to the right and the right hemipenis intromitted.

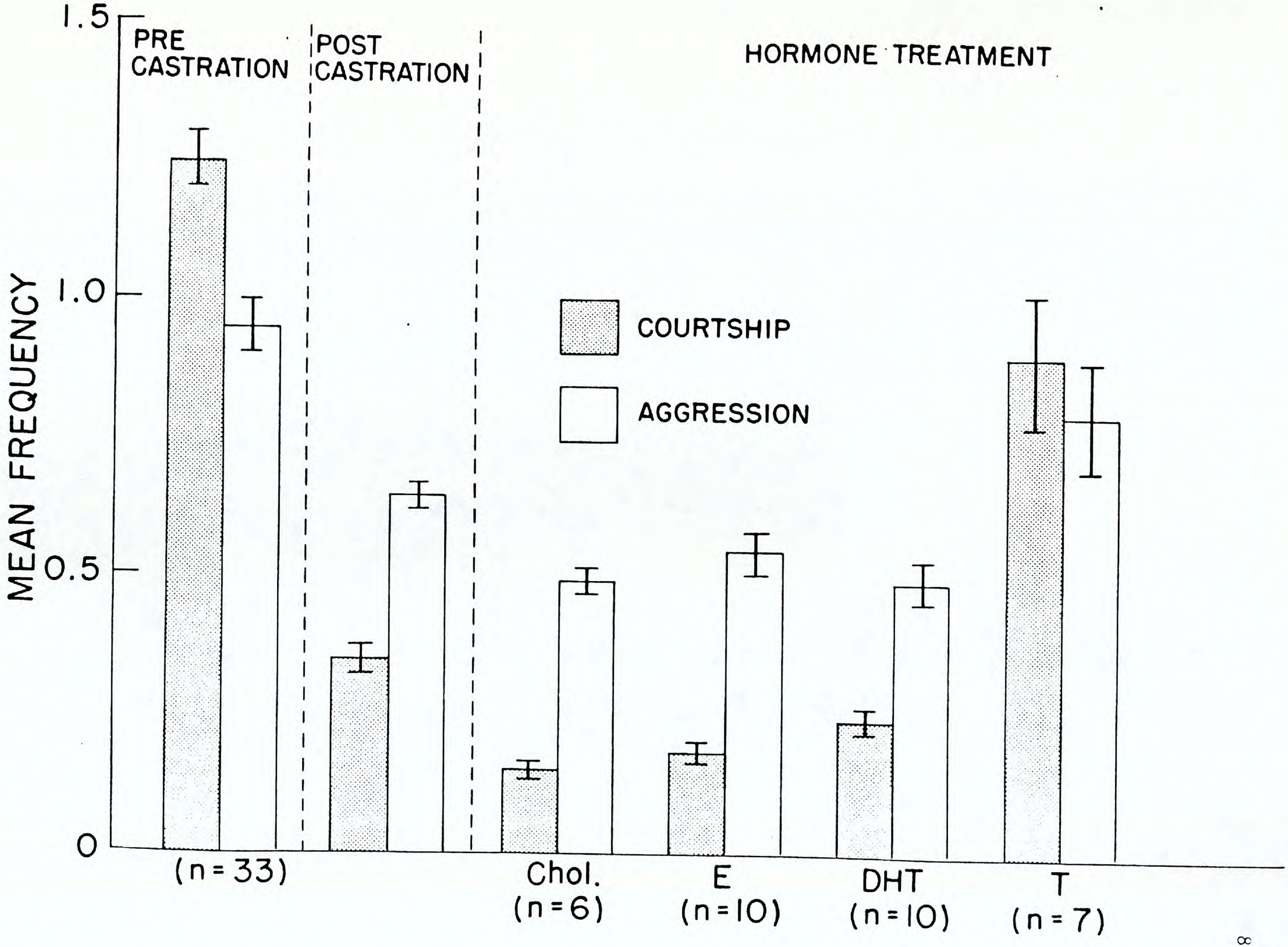
1.5
1.0
0.5
0
MEAN FREQUENCY
PRE CASTRATION
POST CASTRATION
HORMONE TREATMENT
COURTSHIP
AGGRESSION
(n = 33)
Chol. (n = 6)
E (n = 10)
DHT (n = 10)
T (n = 7)

FIG. 1

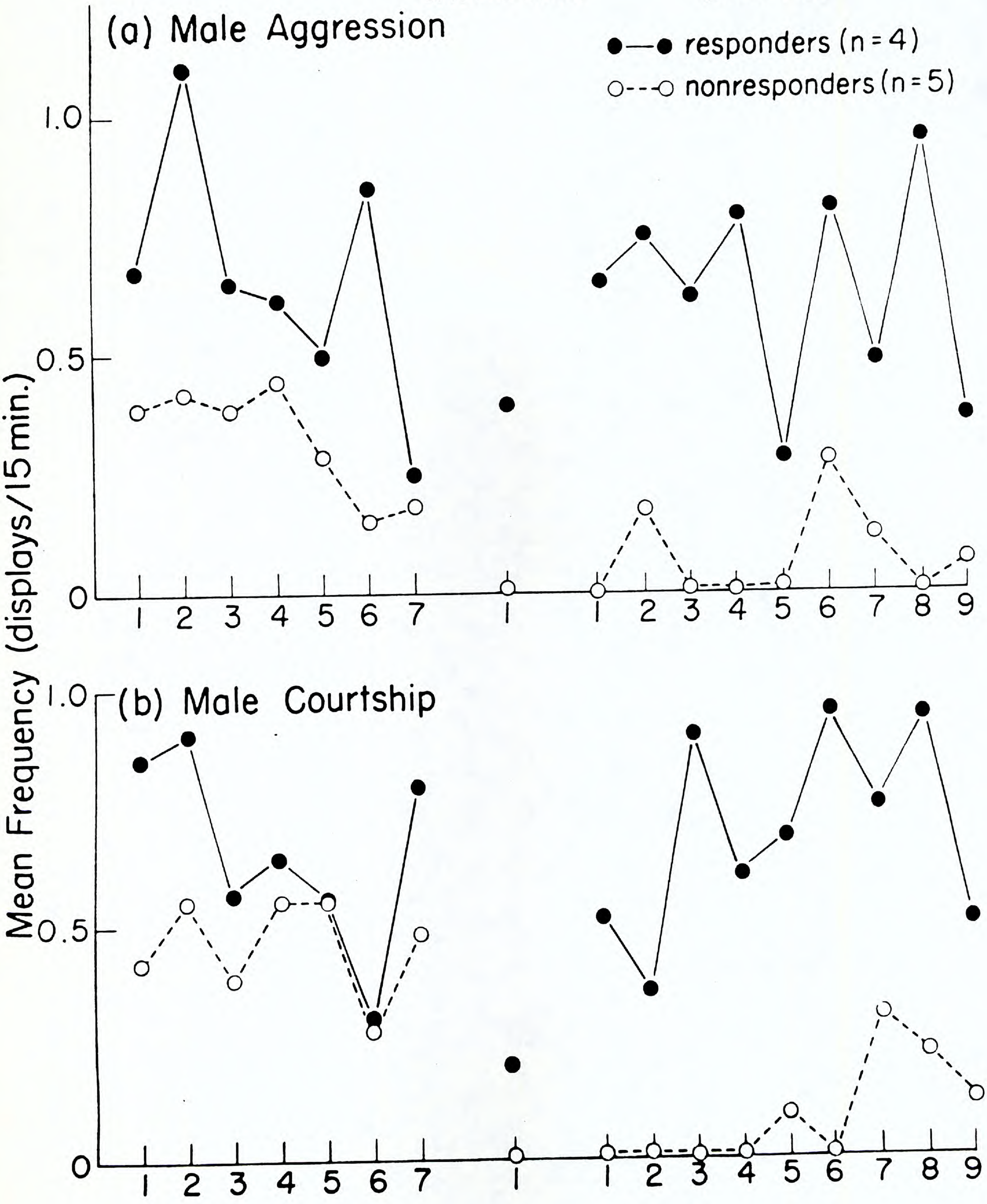
PRE CASTRATION
2 WEEKS POST CASTRATION
HORMONE TREATMENT (DHT + E)
(a) Male Aggression
responders (n = 4)
nonresponders (n = 5)
1.0
0.5
0
Mean Frequency (displays/15 min.)
1 2 3 4 5 6 7
1
1 2 3 4 5 6 7 8 9
(b) Male Courtship
1.0
0.5
0
1 2 3 4 5 6 7
1
1 2 3 4 5 6 7 8 9

FIG. 2

In our examination of the stimulus control of male copulatory behavior, we have made the following discoveries: First, data indicate that most males do not exhibit any preference for either the right or left hemipenis during mating. Although some males may indeed have a preference (if given an extended series of tests, c.f., Males B and C), most males were impressively random in their choice (see Table 1). Secondly, we have found that removal of one hemipenis alters male mating behavior. [For those males that did not exhibit an obvious preference, the hemipenis removed was chosen randomly, whereas in those males that exhibited an apparent preference for one side during the six preoperative mating tests, the preferred hemipenis was removed.] Preliminary data have been conclusive; males that have been unilaterally hemipenectomized only assume a posture which enables them to use the remaining hemipenis (see Table 2). Further, the transition from preoperative random behavior to a postoperative preference occurs immediately, without any obvious "trial and error" on the part of the male.

Unilateral castration has a similar, but not as dramatic, effect on male copulatory behavior. Unilaterally castrated males tend to assume a copulatory posture in which the hemipenis contralateral to the castrated side is used. Since each hemipenis is supplied independently by the vas deferens arising from the ipsilateral testis, it is possible that peripheral feedback from the hemipenes and testes serve to monitor the ability of each testis to deliver mature sperm. We are currently trying to determine if such feedback could be the basis of the alternation of right and left hemipenis observed during successive copulations.

III. Coition-induced inhibition of sexual receptivity.

In a previous study on the behavioral correlates of ovarian follicular maturation in the lizard, A. carolinensis, it was found that sexually receptive females that had been allowed to mate with a sexually active male were no longer receptive when retested 24 hours later. When these females were tested several weeks later, however, they were found to be sexually receptive once again and to contain a large preovulatory follicle. This indicated that mating might serve to inhibit further sexual receptivity within each follicular cycle, but not sexual receptivity during subsequent follicular cycles. Crews (1973, Physiol. Behav.) demonstrated that this was indeed the case, showing that 1) normal mating does inhibit subsequent sexual receptivity during the same follicular cycle, and 2) the transition from sexual receptivity to non-receptivity takes place less than a minute after copulation.

An initial experiment has been completed which suggests that ovarian hormones are centrally involved in coition-induced inhibition. The post-copulatory inhibition was first redocumented by mating five intact females and testing them for sexual receptivity 24 hours after copulation: none of the tested females were found to be receptive 24 hours after mating (see Table 3A).

Table 1. Hemipenile mating preference in Anolis carolinensis
(L = left hemipenis; R = right hemipenis)

Male	Hemipenis used	No. of matings	
		Right	Left
2	L L R L R L R L R L R	5	6
3	L L R L R L	2	4
5	L R R L L L L	2	5
6	L L R L L R R R	4	4
A	R L R L R R	4	2
B	R R R R L R	5	1
C	R R R L R R	5	1
F	L R R R L R	4	2
G	R L R R L L	3	3
H	R L L R R L	3	3
J	R L L R R R	4	2

Table 2. Mating pattern following removal of right or left hemipenis

Male	Hemipenis removed	No. of matings	
		Intact side	hp-x side
3	L	8	0
5	L	8	0
6	L	7	1
B	R	6	0
C	R	8	0
J	R	8	0

Table 3.

Effect of copulation on sexual receptivity of female A. carolinensis.

	Initial Sexual State	Sexual State 24^{h} after copulation
A.	Intact Females (n=5)	0
		0
		0
		0
		0
B.	Intact Females with 6mm EB Implants (n=5)	0
		0
		0
		0
		0
C.	Ovariectomized Females with 6mm EB Implants (n=15)	0
		0
		0
		0
		0
		0
		0
		0
		0
		0
		0
		0
		0
		0

0: Sexually receptive. Will stand for male and arch neck.

X: Sexually inhibited. Runs from male.

Two new groups of females were created: Group I consisted of five intact animals with 6 mm implants of estradiol benzoate (EB), and Group II consisted of 15 ovariectomized females with similar 6 mm EB implants. Pilot experiments had determined that an EB implant consisting of 1.0 mg of EB encased in a silastic capsule with inner diameter .030 mm and length of 6 mm would release sufficient estrogen to make 75% of adult ovariectomized females sexually receptive. All females in both groups were placed individually in cages containing active males until they copulated. Following mating, females were removed and housed individually. All females were retested 24 hours later for sexual receptivity. Tables 3B and C summarize the results: 4 out of 5 intact females with EB implants were unreceptive 24 hours after copulation, while 14 out of 15 ovariectomized females were found to be receptive when retested. As the only difference between the two groups was the presence or absence of ovaries, it seems reasonable to conclude that the ovaries -- and probably ovarian steroids -- are centrally involved with post-copulatory sexual inhibition.

Three related studies are currently being conducted: 1) To evaluate the time course of the post-copulatory inhibition in both intact and ovariectomized females, intact and ovariectomized/EB implanted females are being retested for sexual receptivity at varying intervals after copulation. 2) A second set of experiments is focusing on the physiological mechanisms responsible for maintaining the inhibited state. While we now know that ovarian hormones are involved in maintaining nonreceptivity 24 hours after mating, the mechanism(s) responsible for maintaining nonreceptivity immediately after mating are not entirely clear. Ovarian hormones may be released very shortly after copulation, causing the animal to be sexually inhibited, or alternatively, some exclusively neural mechanism may be inhibiting the female during the earlier stages of the inhibited period. The sexual state of intact/EB implanted females is being compared to that of ovariectomized/EB implanted females 5, 10, 30, 60, and 360 minutes after copulation. In related experiments, 0.5 mg of progesterone injections are being administered following mating. 3) A final study is concentrating on the critical factors in the normal copulatory sequence that initiates the inhibitory response. Crews (1973) has shown that courtship by the male alone is not sufficient to induce sexual inhibition in an intact female. The effectiveness of vagino-cervical stimulation from an artificial hemipenis, and/or the injection of milked ejaculate into the cloaca in initiating nonreceptivity is being determined. The effectiveness of spermless ejaculate (i.e., copulation with a castrated male with a testosterone propionate implant) is also being examined.

IV. Gonadotropin uptake and ovulation.

In adult female A. carolinensis, eggs are generated in one of two ovaries every 10 to 14 days. Ovaries alternate in their production of eggs, so that while the animal is laying an egg every two weeks a single ovary regularly produces a ripe follicle every 20 to 28 days. The following experiment is being carried out to determine the effects of unilateral ovariectomy on the rate of egg production in the contralateral ovary. Forty females have been divided into the following groups: Group I, 10 intact females; Group II, 10 females with sham unilateral ovariectomies, 5 on the right side and 5 on the left side; Group III, 20 females with real unilateral ovariectomies, 10 on

each side. Females are palped every three days to monitor the rate of follicular growth in each ovary. Preliminary data indicate that a single ovary in an intact animal produces an egg every 23 days, while the remaining ovary in a unilaterally ovariectomized animal produces an egg every 17 days. While results are still accumulating, these data confirm Jones' (1975, Gen. Comp. Endocr.) hypothesis that large, preovulatory follicles absorb the bulk of serum gonadotropin and thus determine the rate of egg production. That is, the removal of a single ovary frees gonadotropin, accelerates the growth of follicles in the remaining ovary. When the largest follicle in the remaining ovary is ovulated, all gonadotropin remaining in the blood will be absorbed by follicles in the same ovary, shorting the time it takes the remaining follicles to mature.

V. Neural sites of action of steroid hormones.

Hormones modulate both behavior and pituitary function via their influence on the brain. While the vast majority of research demonstrating this action has been limited to birds and mammals, there is ample evidence to suggest that similar hormone-brain interactions occur in reptiles (see Licht, 1974, for review). In an early attempt to identify and localize steroid-sensitive structures in the lizard brain, Crews, Reboulleau, Garrick, and Feder examined the uptake of high-specific activity estradiol-17β in the hindbrain, midbrain, and forebrain of A. carolinensis using liquid scintillation techniques. Results from this experiment were inconclusive (see Crews, 1975, Science, for data); forebrain did not concentrate estradiol relative to the midbrain or hindbrain. These results should not be interpreted as evidence for a lack of localized uptake of gonadal steroid in the lizard brain, however. If, for example, certain hypothalamic loci concentrated estradiol to a far greater extent than other loci, those data would have been lost when overall forebrain values were calculated. Realizing this, the liquid scintillation procedure has been abandoned and autoradiographic experiment initiated.

In February, 1976, Joan Morrell, Donald Pfaff, and Crews began autoradiographic studies of the localization of hormone-concentrating cells in the brain of A. carolinensis. For these experiments high-specific activity (80 Ci/mmol) estradiol-17β, testosterone, or dihydrotestosterone (100 Ci/50g body weight in absolute alcohol vehicle) was injected into the right fat body of gonadectomized males and females. Lizards were sacrificed two hours after injection by decapitation and the brain plus pituitary quickly removed and frozen. Processing of unfixed, unembedded brains (horizontal and transverse sections) was as described by Morrell (Morrell et al., 1975, J. Comp. Neurol.). Briefly, frozen sections were picked up on emulsion-coated slides in the darkroom under a safelight; slides were stored in light-tight lead boxes. Beginning at two months (April), sample slides were periodically removed and developed and the tissue stained for visualization of hormone-concentrating cells. Because uptake of steroid (as indicated by the intensity of label) was so strong by August, all sections were removed and stained for analysis.

On the basis of previous work with mammals, four species of birds, an amphibian (Xenopus laevis) and a fish (Lepomis cyanellus) (see Morrell et al., 1975 for review), we predicted that the neuroanatomical pattern of hormone concentrating cells in the lizard brain would be similar to those reported for other vertebrate species and thus provide further evidence for what is apparently a phylogenetically stable core system of steroid sensitive sites in the vertebrate brain. Although analysis is still in the preliminary stages, this hypothesis appears to be justified. The following areas have been found to concentrate hormone in both male and female A. carolinensis: preoptic area and tuberal region of the hypothalamus, pituitary, limbic system, and specific regions of the mesencephalon. Further, a distinct pattern has emerged regarding the hormone specificity of uptake; in both males and females, estradiol exhibits the strongest and most specific (highly localized) pattern whereas DHT has a relatively diffuse and weak pattern of uptake.

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ALLEN DENNISON (Dept. of Obstetrics and Gynecology, College of Physicians and Surgeons, Columbia University, New York, New York 10032) while at Harvard studied the species Anolis richardi and A. aeneus in the Grenadines, comparing islands in which the species occur together with those on which aeneus occurs alone.

The available time (December 19, 1974 to January 4, 1975) limited the number of islands it was possible to visit and logistic considerations narrowed the choice further. The following islands were visited:

Bequia (6.8 mi^2) and Carriacou (13 mi^2), two larger two-species islands; Union (2.4 mi^2) and Canouan (2.9 mi^2), two large islands with only aeneus; and the Tobago cays (Petit Bateau and Petit Rameau), small solitary cays.

On each island temperatures were taken, perch height and perch diameter, stomach contents, snout-vent length, femur length, tibia length and head length were recorded.

RESULTS. Dennison's results parallel the findings on Grenada by Schoener and Gorman 1968: aeneus and richardi in sympatry discriminate their niches on several dimensions. There is also evidence that aeneus, where it occurs alone, utilizes portions of resources from which it is excluded in sympatry.

Climate. Richardi shows a marked preference for shade; aeneus shows more tolerance of the sun. The marked absence of richardi in low scrub and its almost complete absence from the parched east sides of Carriacou and Bequia show this immediately. On Carriacou in a damp arroyo, the distribution of the two species conformed to this dichotomy, richardi on the large shady trees in the center of the gulley, aeneus more toward the edge where there are lower bushes and more sun. It was usual to see individuals of both species on the same tree in the arroyo, aeneus in the sun, richardi in the shade of the other side.

This difference is reflected by significantly different cloacal temperatures in the two species. The preference in aeneus seems rather inflexible. Temperatures on one-species islands and two-species islands are indistinguishable, and comparison of scrub and forest temperatures on Carriacou showed no significant difference. The evidence suggests that there is no downward trend for the ecritic temperature of aeneus in released situations. There is little reason to think that such a trend would be adaptive considering that exposed, xeric conditions are, if anything, more prevalent on the solitary islands, which are usually smaller and lacking in the climatic heterogeneity of the two sympatric islands.

Structural habitat. As on Grenada, males of both species perch higher and on larger diameters than females of their species, and richardi males perch higher and on larger diameters than aeneus males. No general comparison can be made between perches of aeneus on two-species or one-species islands; the

one-species islands are too different among themselves. None of the perch tables for single species islands turns up a significant chi-square value when compared with the pooled data from Bequia and Carriacou.

Food utilization. Most lizards take many small insects and few large ones. Male richardi take much the largest prey. Size of prey taken by female richardi and male aeneus with similar head sizes (17-18 mm) is significantly different at a very high level. For prey volume, the very high level of difference is true for head sizes of 13 to 14 mm as well as for those of 17-18 mm. Aeneus, where richardi does not occur, take larger prey and seem to take prey of greater taxonomic diversity.

Size. There is no indication in island comparisons within the Grenada bank that release from competition has resulted in size increases in aeneus on one-species islands. If such a trend exists, it must be presumed that there has been insufficient time for it to become meaningful. Instead, for whatever reason (productivity ?), aeneus shows a clinal decrease in snout-vent length proceeding north from Grenada on the bank. This finding parallels that of Lazell (1972) for trends in coloration: Grenada's rain forests favor brightly colored anoles changing clinally with climate to dull grey anoles on the lowlands of the bank.

There is, however, evidence that head size in aeneus shows an area relation: head size over body size varies inversely with island size. The two extremes in Dennison's data are for Carriacou, a large island, and for Petit Rameau, a small island. For nearly all body sizes, aeneus on Petit Rameau have larger heads than those from Carriacou. This may reflect a parallel difference in the insect faunas correlated with island size.

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NEIL GREENBERG (Laboratory of Brain Evolution and Behavior, National Institute of Mental Health, Bethesda, Maryland) is pursuing a tripartite investigation centered on Anolis carolinensis:

1. A behavior inventory and ethogram. About 90 discrete postures and behavioral events are delineated, and several kinds of quantitative analyses are in progress. For example, over 100 hours of direct observations on a single population have been entered into computer memory (IBM 760) using a computer terminal as an event recorder. This data (15,000 lines) is presently being analyzed with the aid of computer graphics for activity patterns. Preliminary DAP analyses indicate that the "subordinate" head nods may have the same basic pattern as "assertive" pushups. Data is obtained mainly in laboratory environments that simulate natural habitats. Tests of display behavior are conducted in simplified habitats in which dominants are separated by dividers that permit either controlled visual contact or a physical intrusion into an adjacent male's territory. Display behavior tests in which A. carolinensis was confronted with the sympatric congener A. sagrei resulted in significantly fewer fully developed territorial challenges by A. carolinensis, but some components of the display were retained (crests, eyespot). This indicates the possibility of ethologically "dissecting" the display.

Some field work is proposed to corroborate or extend laboratory observations and to permit a closer look at questions that arise from the laboratory data. Behavior patterns of special interest requiring field study include social grooming during ecdysis, social feeding, tongue-touching, and cryptic postures associated with defensive behavior.

2. A forebrain atlas. A special stereotaxic headholder was developed that uses a bite plate as a horizontal reference plane. Lizard heads are decalcified and the brains cut in place. The forebrain possesses a pallium containing three cortical areas; a large mass filling the lateral ventricle (the dorsal ventricular ridge = DVR); and a rostral-ventral paleostriatum. The forebrain is much like that of other lizards observed (e.g., Northcutt, 1967), but the DVR is extraordinarily large, the lateral (piriform) cortex is very reduced, and the "amygdaloid" area (posterior DVR) is very poorly differentiated. The rostral-lateral half of the DVR is richly connected to the lateral forebrain bundle, much like the turtle (Johnston, 1915; Hall and Ebner, 1970), and is very suggestive of avian ectostriatum. Brains stained to reveal regions of ACHE activity indicate that most of the paleostriatum is homologous to the mammalian basal ganglia. Some lizards had olfactory tracts cut in order to help identify certain nuclear groups and determine olfactory input to the forebrain. After staining for degenerated terminals, a projection along the lateral margin of the brain was observed and a compact pathway was revealed in the area of the "amygdala" at the level of the anterior commissure.

3. A neuroethological study of display. Small lesions in the paleostriatum of lizards affect challenge displays while leaving other behavior, including assertive displays, relatively unimpaired. Lesions in adjacent

areas have no effect. This effect is possibly related to injury of the lateral forebrain bundle, a fiber system connecting the DVR to underlying structures. This agrees with a preliminary report of effects on display behavior in monkeys after lesions of specific parts of their striatal complex (MacLean, 1975).

In addition, Greenberg has been involved in editing the Proceedings of a Conference on the Behavior and Neurology of Lizards that the Laboratory of Brain Evolution and Behavior/NIMH and the National Zoo/Smithsonian collaborated on in 1975. Publication is expected before the end of 1977.

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PAUL HERTZ (graduate student, MCZ) is using Anolis to study the very basic problem of variation, looking at it on several levels and in several contexts.

He found his initial inspiration in the paper by Slobodkin and Rappaport (1974) in which a model of adaptive change is applied to the evolutionary reaction of animals to environmental variation over time. Hertz would apply such a model and its predictions to the more tractable problem of environmental variation in space, in practice therefore to the variations of Anolis - ecological, behavioral, morphological, physiological and genetic - across environmental gradients. Hertz starts with the premise that species can adapt to local environmental conditions in a variety of ways and at a number of levels. It is possible to postulate a series of adaptive responses to changes in local conditions ranging from behavioral shifts to physiological acclimatization to more permanent changes in the genetic structure of populations (Leigh, 1971; Slobodkin, 1968; Slobodkin and Rappoport, 1974). Variation between populations, if it is indeed adaptive, can thus be attributed to either the sequential addition of deeper response mechanisms with increasing intensity of selection or to the simultaneous action of several such response systems working on different time scales.

In order to examine these possible causes of geographic variation in a critical manner, it is necessary to look for patterns of variation on a number of different levels in a continuously varying environmental gradient of some sort. Along such an environmental gradient, the sequential addition of different levels of response should result in different populations having different combinations of behavioral, ecological, physiological, morphological and genetic adaptations, whereas simultaneous action should result in clinal variation within each category.

Altitudinal differences provide a physical environmental gradient to which species must adapt. In multi-species communities another factor enters, since some species fail to adopt the option of adaptation to higher altitudes and are confined to the lowlands while others are restricted to middle or high elevations. An altitudinally wide-ranging species thus encounters three gradients over altitude such that thermal stresses should be at a maximum and water stress at a minimum at high altitudes, whereas interspecific competitive interactions should decline or alter with species replacements.

In the West Indies, there are both single species and two species islands with considerable relief - the Lesser Antilles - and the complex multi-species islands of the Greater Antilles. There is the possibility, therefore, to compare populations both within and between species at a variety of altitudes, and in a variety of competitive contexts, and the consequent opportunity - so one hopes - to discover what factors limit or modify species with increasing altitude. Data on Lesser Antillean Anolis (from one species islands), when compared with that for species from the complex communities of the Greater Antilles, should answer the question whether intrapopulational changes over altitude are to be attributed to the differing climatic regimes or to differing competitive circumstances.

The following details his general protocol:

Techniques I. Field studies.

Hertz first selects for any area three or four localities at different elevations which are vegetationally and structurally as similar as possible. At each of these he does intensive sampling. For each anole captured he records sex, snout-vent length, tail length, body temperature, air temperature, perch height, perch diameter, position with respect to available basking sites, weather conditions at the time of capture and time of day.

Hourly censuses are taken of all lizards (not merely anoles) at each locality and from dawn to dusk during at least two days.

Techniques II. Morphometric analyses.

Collection of large series for laboratory studies are made (necessarily on completion of the field study). Preservation of one sample (80-120 animals per locality) of the animal is done immediately after capture to permit eventual analysis of stomach contents. On these same specimens more than 20 morphological measurements (including scale counts, counts of toe lamellae and measurements of body proportions) are taken.

Techniques III. Physiological studies.

Hertz collects a final series of males from each locality for an analysis of sensitivity to water loss and heat stress. He routinely pinpoints the following parameters: experimental voluntary maximum temperature, critical thermal maximum, lethal maximum, rates of water loss and average proportion of body weight lost (to desiccation) at death.

Techniques IV. Electrophoretic analyses.

Another set of animals (at least 30 animals per locality) is frozen for future electrophoretic study. Twenty-five proteins are routinely assayed. Hertz will not only survey interpopulation differentiation but will be able to evaluate genetic variability of the populations as well.

Utilization of all four of these techniques should permit comparison of levels of variability (in response to altitude) of ecology, morphology, physiology and gene products, all done for the same populations and, in part, for the same individuals.

Hertz's thesis will involve the analysis of altitudinal variation and local adaptation in six West Indian species and species pairs. In Hispaniola, in addition to the data already gathered on the grass anole, A. semilineatus, he has worked on the trunk-ground anole, A. cybotes which, like A. semilineatus, has an altitudinal range of over 5,000 feet. Again like A. semilineatus, A. cybotes has sympatric or parapatric siblings with significantly more limited ranges. In Puerto Rico, species pairs of both ecological types are available:

in grass anoles the primarily lowland A. pulchellus and the primarily montane A. krugi, and in trunk-ground anoles the primarily lowland A. cristatellus and the primarily montane A. gundlachi. (In both species pairs the montane and lowland species overlap widely - but segregate by climatic habitat - at middle elevations.) Hertz regards a fifth species as relevant to his story in Puerto Rico - the green trunk-crown species A. evermanni - which is widely sympatric to gundlachi.

In Martinique - a single species island - A. roquet shows marked geographic variation in color, both altitudinally and horizontally (Lazell, 1972). Hertz has run a transect from lowland to highland and hence across the border between a high altitude subspecies - summus - as recognized by Lazell and a lowland subspecies - majolgris.

Although much of the data is as yet unanalyzed, a number of patterns have emerged from preliminary analysis:

Body size: As in semilineatus (see below), the body size of cybotes increases with altitude. Cybotes is replaced at high altitudes by montane derivatives which are smaller than any populations of cybotes itself. The size difference is therefore greatest in the zone of contact. Although the small size of the montane species may be an adaptation to limited opportunities for basking, examination of the ecological relationships where a montane species contacts cybotes should clarify the possible role of character displacement in the size relationships of these species. As suggested below, the body size cline in semilineatus may be due in part to a response to competitive pressure from olssoni, a lowland grass anole. The morphological data on roquet and gundlachi are as yet mostly unanalyzed. Hertz has, however, demonstrated that body ornamentation in male gundlachi is most evident in populations at lower elevations. Animals at the lower end of the species' altitudinal range more frequently have bright lateral spots and tail crests (as well as larger crests) than do those at high elevations. Since populations are densest and most exposed to possible heat stress at the lower elevations, Hertz believes that this ornamentation may be the product of sexual selection or it may serve a thermoregulatory function. He is planning some physiological experiments to determine whether or not tail crests affect the heating and colling rates of the large males.

Body temperatures: On Martinique, Hertz has found that the single species of anole, roquet, basks significantly more often at middle and high elevations than in the lowlands. Although basking behavior compensates for the decline in ambient temperature at middle elevations, nearly continuous cloud cover forces the montane population to have a mean body temperature about 4^0 C cooler than the lowland one. In Puerto Rico, Anolis gundlachi shows a very different pattern: there is no strong tendency to thermoregulate in any population and mean body temperatures decline steadily with increasing altitude. It is clear that gundlachi is far more passive thermally than roquet and body temperatures are quite low throughout the range. The two other Puerto Rican species examined, cristatellus and evermanni, show different trends. Cristatellus thermoregulates to some degree in the lowlands and body temperatures tend to

be much higher than those of the upland species. Evermanni body temperatures are higher than those of gundlachi because these animals actively seek basking sites at higher perches than do gundlachi in the same habitats, but evermanni tends also to thermoconformation.

Activity cycles: Anolis roquet on Martinique shows a shift in activity cycles over altitude. Lowland populations show a strongly bimodal pattern, with peaks in morning and afternoon but with some activity for 12 hours. A bit higher (350 m), the pattern becomes unimodal, with the single peak near the middle of the 12-hour day. At yet higher elevations (650 m), the period of daily activity is reduced to 10 hours and the lizards seem to be equally active throughout the day. Gundlachi on Puerto Rico shows a somewhat different pattern, with more or less unimodal activity at 270 m, becoming bimodal at 480 m and 675 m, and returning to unimodality at 850 m with perhaps a slight reduction in total time of activity through the day. Anolis evermanni shows a midday peak in its activity at 480 and 675 m, but the total activity period is shorter than that of gundlachi. Hertz believes that the addition of evermanni as a significant competitor may be responsible for the bimodal activity of gundlachi at the two middle localities; it might otherwise be expected to have invariant activity patterns since it is nowhere dependent upon basking for thermoregulation.

Sensitivity to heat stress: A. gundlachi is an anole restricted essentially to dark forests. A. cristatellus, which in some places reaches equally high altitudes, changes its climatic habitat with altitude. Huey and Webster and also Gorman have confirmed Rand's prediction of physiological differences between the two species and that cristatellus does not alter its heat sensitivity with increasing altitude, probably because of its shift in climatic habitat. Hertz and some of his students in Puerto Rico have now shown that there are large variations in CTM among samples of gundlachi from different elevations. The variation is clinal, such that intermediate elevation populations resemble those at either end of the transect, but that the extreme populations are very different from each other. There is, however, no variation in either voluntary maximum or lethal temperatures. A. roquet shows a rather different, but equally neat pattern of geographic variation in heat stress parameters. Hertz surveyed two pure subspecies, one lowland and one montane, and a series of intergrade populations from the lowlands to intermediate elevation populations. The experimental voluntary maximum of the pure lowland population is different from those of all other populations surveyed so that the introduction of "montane genes" significantly depresses the temperatures that the animals are willing to accept. The panting response shows an exactly opposite trend: pure montane populations (identified on the basis of Lazell's designations based on color) pant at lower temperatures than do any populations which contain any lowland (majolgris) genes. Critical thermal maximum varies altitudinally, much like that in gundlachi, but the results are not quite as neat as for that species. Measurements of lethal temperatures demonstrate subspecific differentiation: the majolgris sample can stand higher temperatures than can intergrades which are, in turn, less sensitive than the pure montane animals. Hertz has studied similar phenomena in the cybotoids of Hispaniola and the grass anoles of both Hispaniola and Puerto Rico, and his analyses of these data will be forthcoming.

Sensitivity to desiccation. Hertz and some of his students in Puerto Rico have also examined rates of desiccation and sensitivity to desiccation in A. gundlachi. The results are rather like those for the heat sensitivity studies. While animals from different elevations show no differences in their vital limits, i.e. their tolerance to desiccation, there are large differences in the rates at which small males from different elevations lose water in desiccating environments. The general trend is for small males from high elevations to lose water faster than those from lower on the mountain, but large males do not appear to show such variation. The net result is that body size has a greater effect on the relative rates of water loss in montane gundlachi than in those from lower elevations. Hertz has independently undertaken comparable studies on the other species that he has studied, and these results will be forthcoming as well.

Hertz concentrated his research efforts during 1974 and early 1975 on the systematics and ecology of the Anolis semilineatus complex of Hispaniola. In addition to collecting (with Raymond Huey, Ernest Williams and Robert Holt) some of the first statistically useful series in the species complex, Hertz has morphological, genetical, and ecological data to approach problems posed by the systematics and ecology of these species.

Hertz uses two lines of evidence to argue that A. cochranae is not a good species. First, according to the electrophoretic evidence, it is (within the limits usual for intra-species variation) essentially identical to five other white-dewlapped populations, including one collected from an area near sea level . Secondly, there is overlap in the one scale character upon which the description of cochranae was based. Williams and Rand (1961) described cochranae as having 10-12 enlarged dorsal scales in a standard distance and semilineatus as having 14-17. The newly available material shows that the differentiation into two categories is not real and that the low scale counts (and therefore large dorsal scales of "cochranae")must be explained as clinal variations in semilineatus.

With the data provided by the collection of the summer of 1974, Hertz has been able to show that, in the white-dewlapped grass anoles of the "North Island" of Hispaniola (A. semilineatus and its synonym A. "cochranae"), body sizes and the relative sizes of the enlarged middorsal scales increase monotonically in both sexes with elevation. Both characters show substantial correlation with elevation. Males and females increase body size with elevation at the same rate so that the degree of sexual dimorphism is not substantially different at different altitudes.

Anolis olssoni, on the other hand, shows no systematic variation of these characters with elevation. There is no significant correlation for either sex of body size or scale size with the altitudes at which populations were sampled.

A survey of the localities from which the two species are represented in the major U.S. collections (MCZ, AMNH, USNM, Albert Schwartz Field Series)

has enabled him to pinpoint 16 likely areas of sympatry or parapatry. In the past, researchers have thought that olssoni was restricted to more xeric and semilineatus to more mesic situations, such that sympatry was either rare or nonexistent. However, this is clearly not the case. The field party, of which Hertz was a member, located two new broad zones of sympatry; at one of these areas - the road from the airport to Sto Domingo - the species were regularly sympatric over a 13 kilometer transect, specimens from the two species being repeatedly caught within a few meters of each other. More recent field work (by Hertz and others in 1976), however, suggests that grass anole populations on Hispaniola are extremely labile: Hertz was unable to find any grass anoles in the area where the two species were formerly abundant and syntopic. Though he cannot rule out the possibility of competitive extinction of both species, Hertz believes that the grass anoles may be classic "tramp" or "fugitive" species, utilizing changing habitats briefly. He found no olssoni near Santo Domingo in 1976, but did discover a dense population of semilineatus several kilometers east of the locality that provided large series of both species in 1974.

The extensive though transient sympatry of the two species poses the issue of the mechanism of resource partitioning in these animals. Hertz believes (but lacks the data necessary to constitute a proof) that the cline in semilineatus body size is a response to competitive pressure from olssoni. Since the latter species is predominantly found at elevations below 500 meters, semilineatus may be forced to a smaller size in the lowlands where the likelihood of sympatry with olssoni is high. At middle to high elevations (500 - 1300 meters), semilineatus may undergo ecological release in the absence of olssoni and attain a body size (about 15% larger than in the lowlands) more suitable for the capture of a larger range of prey sizes. Since thermal constraints at high elevations may allow hunting activity for shorter periods of time than in the lowlands, it might be selectively advantageous for the animals to be able to utilize a larger range of available prey at any given time. Planned (but not imminent) collections of semilineatus from the Tirubon Peninsula of Haiti (far from the nearest olssoni locality) should enable him to confirm or refute his hypothesis about character displacement in body size. For the moment, Hertz has only one explanation for the concordant increase in relative scale size in semilineatus. He thinks that larger middorsal scales may allow the larger animals at high elevations to heat faster while basking. Since there is a moderate correlation (r=.75) of snout-vent length and relative scale size between populations, it is possible that they are related in a common selective regime. Hertz hopes to perform a series of experiments to determine the effect of dorsal scale size and body size on the heating and cooling rates of lizards. Although much is known about the heating and cooling rates at various body sizes, the effect of scale size on the system is as yet an unexplored area of research.

Hertz has noted an additional pattern of variation in semilineatus that may be related to a character displacement phenomenon. In both species, the middorsal stripe may be distinct (either a light stripe bordered by darker parallel lines or a series of chevrons which are connected medially into a

very light central stripe) or indistinct (either an ill-defined series of chevrons lacking the light colored medial connections or a chalky middorsal blush). At 10 north island localities where the two species appear to be sympatric (defined as collected within a kilometer of each other), olssoni is almost always distinctly striped: 95% of 165 animals have a pronounced middorsal stripe. Semilineatus, in contrast, usually lacks a distinct stripe at these localities: only 21% of 117 animals show the character. At Les Platons, near the tip of the Tiburon Peninsula, however, semilineatus, allopatric to olssoni, shows marked middorsal striping in 83% of 34 animals in the series. And 84% of the 44 adults in a sample of semilineatus (see below) from Balneario Rio Grande, near Constanza (allopatric to olssoni), show a marked middorsal stripe. Similarly, 10 individuals of semilineatus out of a sample of 11 specimens (91%) from the Ile de la Tortue, an island on which olssoni has never been recorded, have distinct striping. The situation at a south island locality of sympatry (Petionville area, including Boutillier Road) is somewhat confusing: 67% of 51 specimens of semilineatus and 60% of 51 specimens of olssoni show distinct stripes. It is possible that the invasion of this limited part of the south island by olssoni has been too recent for the evolution of a character displacement of dorsal pattern. It is perhaps just as likely, however, that semilineatus and olssoni have not been truly syntopic in the Petionville area for a long time and that lack of contact has left the striping patterns unchanged. The changes in striping frequency in semilineatus between areas of sympatry and allopatry of olssoni suggest that the stripe may function as a species recognition character in contexts in which dewlaps are not used.

While in the field during the summer of 1974, Hertz and Huey collected large samples of body and air temperatures for semilineatus and olssoni at the large area of sympatry. Both species are eurythermic and are active over a wide range of body temperatures (approximately 10° C; both species react similarly to the range of air temperatures in the habitat (slopes of the BT vs AT regressions are not statistically different). However, the elevations of the separate regression lines are different (although the body temperatures overlap substantially), indicating that at a given air temperature, olssoni tends to have a higher body temperature. The differences in the temperatures are emphasized by the fact that semilineatus, the smaller of two very small species, would be the more likely to heat in the hand (while body temperatures are measured), thus reducing the actual temperature difference between them. Hertz cautiously suggests that the body temperature differences and the fact that olssoni is the larger species (and therefore heats and cools more slowly) may indicate that olssoni perches in (and therefore hunts from) more open spaces in a given area than does semilineatus.

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ROBERT HOLT (graduate student, Harvard University) reports on his recent field research:

I am interested in species border phenomena. During the summers of 1975 and 1976 I have studied the ecology and distribution of three species of Lesser Antillean Anolis that provide interesting material for the study of factors that limit species' distributions. Anolis aeneus and A. trinitatis are believed to be introduced onto the continental island of Trinidad from the oceanic islands of Grenada and St. Vincent. The Anolis richardi on Tobago are very similar to richardi from Grenada. The lack of morphological differentiation suggests that all three species are relatively recent colonizers. As compared with their Grenadan counterparts, the introduced aeneus and richardi show sharply circumscribed ranges; as discussed below, these limits are not due to competitive interactions with other lizards. By contrast, A. trinitatis exists on Trinidad as scattered enclaves within the range of aeneus; the two species are mutually exclusive with narrow bands of overlap, and aeneus appears to be slowly pushing trinitatis to extinction.

Anolis richardi. Several authors have noted that richardi on its native island of Grenada is ubiquitous, ranging through many habitats from xeric scrub forest at Pt. Saline to high wet forest near Grand Etang. There is one puzzling feature of its distribution that has not been noted. Since I wished to compare comparable habitats on Grenada and Tobago, I searched for patches of near-virgin habitat (with the assistance of local foresters). I found such patches on Mt. Delice (a dry forest) and in the Grand Etang Forest Reserve (a wet forest). Anolis richardi was conspicuously less common in these patches than in most other wooded habitats on Grenada. This is somewhat peculiar, since there are no obvious competitors or predators in virgin forest that are more common than in disturbed habitats. It is possible that insect productivity is less in these forests (Janzen, 1973). I suspect that the anoline abundance of the West Indies (at least in wet habitats of the Lesser Antilles) may in part be the result of massive disturbance during the last five centuries and may not accurately reflect the conditions in which these anoles evolved.

The distribution of richardi on Tobago presents quite a different pattern. As noted by Lazell (1972), richardi is common all along the southern coast. The animals can be observed in areas near human habitation, or in coconut groves. But in less disturbed habitats with more structural complexity, the anoles are markedly scarce. For example, at the Botanic Gardens in Scarborough a range of habitats varying in their disturbance is available. The anoles are present in some numbers within the gardens themselves. As one walks into the wooded hills behind the gardens, the density of visible anoles gradually decreases; a hundred yards or so inside the forest not a single anole is visible. The remarkable thing about this situation is that these wooded hillsides look similar to those Grenadan habitats in which richardi is most common; the woods are far from virgin, since many trees have been cut and there is a good deal of patchiness, clearings of varying size being scattered throughout. On one long hike in the highlands, I did not see a single richardi; at the Alefounder Estate in the lowlands (one of the few

areas left unharmed by the hurricane), richardi were common in the immediate vicinity of the estate buildings; only one anole was seen in the forest. Thus, there is a very clear large reduction in anoline densities between Tobago and Grenada in forested habitats; in habitats near human habitation, and in coconut groves, the densities on the two islands are comparable.

Diffuse interactions with other Tobagan species may have led to the reduction in the habitat range of richardi. Grenada and Tobago have the same overall climate, and the vegetation is similar, but Tobago has a substantially richer fauna of birds and snakes. Competition with other lizards cannot explain the habitat limitation; no other anole is present, and the only other arboreal lizard on Tobago is Iguana iguana - which is also on Grenada and is not likely to compete directly with richardi, anyway.

Anolis aeneus. The preferred habitat of aeneus in Grenada is scrubby woodland with plenty of small trunks; they are abundant in disturbed habitats all over the island. One might surmise that the introduced aeneus of Trinidad would be widespread over the island wherever second growth occurs. This is not the case. There are two striking differences between the distribution of aeneus on Trinidad and its distribution on Grenada. On Grenada, aeneus has a continuous distribution. On Trinidad a number of disjunct populations exist, some separated by many miles from their nearest neighbor. For example, the population at Maracas Bay is restricted to a small grove of coconuts at a public beach park; a tall heavily wooded mountain range separates this population from the main range of the species. Second, aeneus on Trinidad occupies a much narrower range of habitats than on Grenada. The species behaves as a vertebrate weed, its populations occurring only in artificial habitats provided by man - in his suburban gardens, in his public parks, in coconut groves and, sometimes, in overgrown, abandoned lots. This close association with man probably explains the haphazard, overall distribution of the species. The overall shape of the distribution is likely the result of passive dispersal by man. The habitat restriction on Trinidad as compared with Grenada is of greater intrinsic interest. The borders of populations are often surprisingly sharp. I have found numerous examples of populations thriving in backyards or parks immediately adjacent to bushy woodlots, in which not a single anole could be found in the woodlot. In superficially similar areas on Grenada, aeneus is swarming. The absence of aeneus from apparently accessible, suitable habitats is characteristic throughout the range of aeneus in Trinidad. I feel that this habitat restriction is caused by the cumulative effects of a large number of native species, particularly snakes and avian predators. My evidence for this is mostly indirect. Several other, alternate hypotheses can be eliminated. For example, the density of anoles might simply be tracing a gross pattern of insect abundance. By sampling insect density with Tanglefoot and sweep netting, I have shown that this is not the case. On Grenada, the density of aeneus seems to be correlated with insect density; in Trinidad, along a transect from an inhabited area into an adjacent patch of second growth, insect density increased but aeneus decreased to zero. Direct competition with another species of lizard cannot explain the limited habitat range;

the only native anole on Trinidad, chrysolepis, is not found in these habitats, and the other arboreal lizards either overlap extensively with aeneus (Gonatodes) or are also not found in these areas of bushy second growth (Polychrus and Plica).

Grenada has six species of snake; Trinidad has about 40 species. There is an order of magnitude difference in bird species, too. Forty-one species of bird on Trinidad are known to include small lizards in their diet; several of these are common residents of second growth (e.g. antshrikes). Between Grenada and Trinidad there is a phenomenal increase in the diversity of small insectivorous birds which could both compete with adult aeneus and prey on juveniles; many of these are common in second growth and forage in just those places utilized by aeneus - along trunks and in the interior of foliage. It is a priori reasonable, therefore, to expect that aeneus on Trinidad faces a whole spectrum of enemies, absent on Grenada, that limit its distribution.

To provide indirect evidence for this hypothesis, I searched out sites which might be expected to have a depauperate fauna. I have found aeneus on a chain of islands west of Port-of-Spain (Fig. 1). The bird species of these islands follows the usual species-area relationship. As one goes down this island chain in order of decreasing island size, the density and habitat range of aeneus increases in a regular fashion. On Monos, anoles are restricted to near human habitation. On Gasparee, aeneus does penetrate roughly a hundred yards into wooded areas adjacent to yard populations, but in low densities. The entire surface of Cronstadt has resident anoles. On the small Five Islands, aeneus reaches its highest abundance. On Caledonia, as on Grenada, the density of anoles seems to roughly track insect abundance; this pattern does not hold on Gasparee. I also censused the birds at these sites. On Caledonia, the bird list is reminiscent of the Grenadan avifauna, with few foliage-gleaners or trunk-feeders, and no species likely to prey on aeneus. My mark-recapture data suggest that adult survivorship is lower on Cronstadt than on Caledonia; several species of presumed predators and competitors are present on Cronstadt. Thus, aeneus on these offshore islands shows a regular pattern of habitat expansion concordant with a decrease in bird species diversity.

I have also studied the distributional pattern of aeneus on habitat 'islands' of second growth found scattered throughout settled areas near Port-of-Spain. These patches are usually sharply defined. Most of the land is kept clear of thick growth by the owners of the lots; abandoned lots, and those have never been cleared, are covered with dense vegetation. I characterized each patch by its area, distance to continuous vegetational cover, distance to yard populations of aeneus, and several indices of vegetational density, cover, and height; I also listed bird and lizard species seen. From equilibrium theories of island biogeography, it is to be expected that the diversity of potential predators or competitors will decrease as the size of the patch decreases or the distance of the patch from large, continuous tracts of similar vegetation increases. Given that this expectation is reasonable, I predicted that aeneus would be found in high densities in small

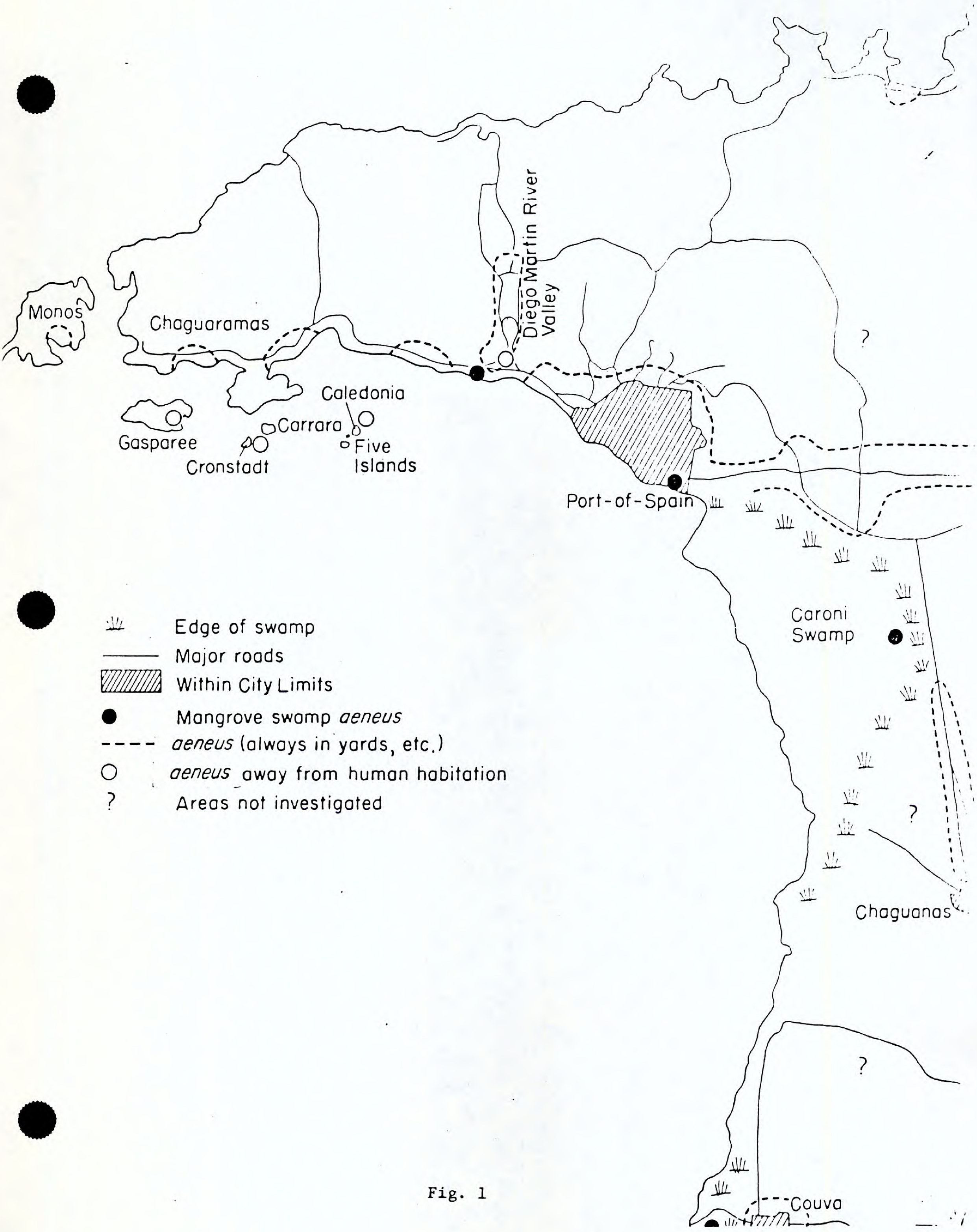
Monos
Chaguaramas
Diego Martin River Valley
Caledonia
Carrara
Gasparee
Cronstadt
Five Islands
Port-of-Spain
Caroni Swamp
Chaguanas
Couva
?
?
?
Edge of swamp
Major roads
Within City Limits
Mangrove swamp aeneus
aeneus (always in yards, etc.)
aeneus away from human habitation
? Areas not investigated

Fig. 1

patches, absent from large patches (or present only along the edge, if adjacent to a yard population), and present in lower abundance in patches of intermediate size, particularly patches that are isolated. All these predictions were found to hold. Most patches less than 1000 m^2 are occupied by aeneus; those that are not occupied are either immediately adjacent to large areas of second growth, or are distant from yard populations of aeneus. Patches between 1000 and 5000 m^2 are less often occupied; those patches with aeneus tend to be more isolated. In those patches that are occupied, the density of aeneus is less than in patches below 1000 m^2 in size. I did not find aeneus in any patch above 5000 m^2 in size. There does not appear to be a correlation between aeneus' presence and any attribute of the vegetation I could measure. In like manner, I made a survey of habitat 'islands' near St. George's, Grenada. There, aeneus is present regardless of the size or degree of isolation of the patch.

Anolis trinitatis. Gorman has investigated several aspects of the interaction between Anolis aeneus and A. trinitatis on Trinidad. He has pointed out that the two species hybridize freely, the hybrids are sterile, or nearly so, and there is little overlap between the ranges of the two species. This situation is intriguing for two reasons. First, we expect strong selection for the development of reproductive isolating mechanisms, yet both anoles have been on Trinidad for a century or more, and their striking visual distinctness would seem to make them ideally pre-adapted for the development of such mechanisms - but they have not. Second, they provide a pleasing example of competitive exclusion in action. Victor Quesnel has kindly provided me with a set of maps that he and Garth Underwood had made during the late 1950's. These maps show in exquisite detail the distribution of both species in Port-of-Spain and St. Augustine. During August, 1976, I re-mapped the distribution of trinitatis in Port-of-Spain. Previously, it existed in four enclaves more or less surrounded by aeneus. I found that the smaller two of the four enclaves had disappeared; the larger two had shrunk considerably in size. From the apparent rate of shrinkage of the two larger enclaves, one would have predicted the disappearance of the two smaller ones. The largest enclave was bounded on the east by an enormous grassy field, on the west by a large concrete ditch, and on the other two sides by aeneus. The two edges bordered by aeneus had shrunk, the other two had not. This strongly suggests that the range contraction is due to interaction with aeneus rather than some unknown environmental change. The two species show great overlap in their structural niche, in the time of day at which they are active, and in size. In the narrow zone of spatial overlap, I observed many instances of interspecific aggression, both between males and between females. The density of lizards was correlated with the quantity of vegetation available. The width of the zone of overlap varied inversely with the total number of lizards observed.

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THOMAS JENSSEN (Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061) has sent in the following.

For the present Anolis Newsletter, I thought I would provide a brief overview of my past and present studies on anoline displays. Enough species have finally been studied to permit an initial discussion of trends which have appeared (though exceptions abound).

Let us start with an historical perspective. First, display analysis begins with the important work of Charles C. Carpenter. He and his students have demonstrated that iguanid lizards have stereotyped display behavior and that the patterning of these vertical body movements through time produces patterns unique for each species. Lacking in these early investigations, however, was an appreciation for variability in display behavior. Probably because of the species initially studied, there prevails even to this date a generalization that a species performs only a single unique display pattern. This generalization does not apply to most anoline species, and may in fact be incorrect for many other iguanid lizards.

We will now explore some landmarks of my work with anoline display behavior by walking some old pathways, treading recently opened areas, and peering into a few thorny thickets:

1. Signature display and display modifiers. Carpenter's idea that each species has its unique display-action-pattern (DAP) remains valid. There may be a number of distinct DAPs in a species' repertoire, but the one which is used in an assertion contest (e.g. performed by a male while patrolling his territory with no conspecific in view) can be considered the signature display pattern and basic to the species' repertoire.

Regardless of species, this functional display type is subject to modification by the optional addition of certain postures, or "static modifiers" (e.g. lateral flattening of body, raised nuchal crest, gorged throat, possibly tongue protrusion), and movements, or "dynamic modifiers" (e.g. exaggerated limb extension, introductory body movements immediately preceding the stereotyped display pattern, possibly several repetitions of the pattern's concluding body movements).

Besides the signature display, the lizards also add modifiers onto the other display patterns of their repertoire. However, if a particular display pattern is only used during high arousal situations (close contact male-male confrontations), the modifiers may approach a 100% frequency of occurrence with that type of display. Under these conditions the distinction between whether the modifier is really a modifier or an integral part of the display becomes blurred.

An example of this point is the question whether "raised nuchal crest" is a static modifier in Anolis limifrons C, D, and E displays. A raised crest was only occasionally seen in the species' A and B displays, but was always

seen in the C, D, and E displays (Hover and Jenssen, 1977, Behaviour 58: 173-191) (Fig. 1). These last three display types are only observed as males approach each other, ensuring a situation of high arousal.

Another example concerns dynamic modifiers of introductory movements. Exaggerated head rolling or bowing are commonly tacked onto the front of a display type by many species as the lizards become more aroused. In Anolis nebulosus (Jenssen, 1970, J. Herpetology 4: 1-38, p. 24) the bowing appearing at the beginning of the signature display pattern was used to make a distinction between two display types - the pattern used in a challenge context (bowing and signature pattern), and the pattern which functions as the species' signature display. From subsequent experience with other species, however, I now view A. nebulosus as having only one unique pattern to which an introductory bowing movement (i.e. a dynamic modifier) is added during greater arousal. The bowing in A. nebulosus is not sufficiently stereotyped, in my judgment, to consider it an element of another predictable pattern.

From the above two examples, the thorny question arises: When does an optional movement or posture slide from a status of modifier to a permanent component of a stereotyped display pattern? It is apparent that any generalization is bound to reveal its synthetic construction at times. Fortunately, the exceptions so far are not a frequent problem, and the concept of modifiers remains valuable in evaluating display variability.

Though requiring more experimental evidence, it appears that the appearance of modifiers indicates a more aroused animal. As such, modifiers undoubtedly play a strong role in communication function and enhance or change the basic message of the stereotyped behavior to which they are added.

We are probably seeing within each display type a graded signal based on the absence or presence of modifier combinations and, in some species, a temporal variability in the display performance.

2. Display repertoire size. My criteria for determining repertoire size are restrictive and produce conservative results. The display behavior that I count to determine a species' repertoire size are only those species-unique head and/or dewlap movements that are stereotyped and descriptively distinct from each other. I do not count a pattern more than once even though it may appear in a host of contexts (e.g. assertive, courtship, challenge) and may have a constellation of possible modifier combinations associated with it.

Behaviors excluded from repertoire size are those which are not obviously stereotyped and are interspecifically shared. For example, common to all anoles I have seen and certainly common to most of the Anolis species is the use of dewlap movement divorced from stereotyped body movement. For the most part such "dewlapping" is non-stereotyped and can appear: (1) after eating; (2) during shedding; (3) when the animal enters a part of its domain with which it was previously out of visual contact; and (4) as a reaction to the beginning or tailing off of a social encounter. Undoubtedly there are a few

anoles whose dewlapping may be stereotyped and an important display of its formal repertoire. With the exception of these species, I do not consider dewlapping in the discussion of repertoire size. I also exclude the rapid, shallow head bobs common to the courtship context of iguanid lizards in general.

On these conservative principles, every anole I have studied (with the possible exception of A. nebulosus) has at least two display types. So far the largest repertoires are those of A. limifrons with five (Jenssen and Hover, 1976, Behaviour 57: 227-240; Hover and Jenssen, 1976, Behaviour 58: 173-191) and A. townsendi with at least four (Jennsen and Rothblum, Copeia 1977: 103-109).

Another trend in anole repertoires is that there is a species-unique signature display pattern (A) and a second pattern (B) which differs in subtle fashion from the A type. This B type is usually restricted to agonistic interactions, while the A type is used in assertion, courtship, and initial challenge contexts. Examples of this close descriptive relationship are the A and B displays of A. limifrons, A. townsendi, A. grahami, and A. garmani (Fig. 2) (from Jenssen, 1977, Amer. Zool. 17: 203-215).

If one believes that a repertoire of genetically fixed signals evolves from small to large, it is not unreasonable to expect the evolution of subsequent signals to share many aspects of the previous signal or signals. It is necessary to be alert for small, but statistically significant, distinctions in movement patterns. To verify if any of these patterns are functionally distinct, controlled social situations must be provided to determine if the two displays are used within different circumstances. Larger differences between displays of a repertoire may evolve by welding pre-existing display acts together in a novel combination. For example, it appears that the elaborate A. limifrons display was produced by taking its B display, fusing a series of 4-legged pushups to it, and ending the sequence with the A pattern (Fig. 1).

Possibly reflecting a similar evolutionary process for increasing repertoire size, Jenssen and Rothblum (1977, Copeia 1977: 103-109) point out how A. townsendi and A. limifrons repertoires resemble each other. The repertoires contain a species-unique signature display (A), a second display type (B) which closely resembles the A pattern, and a third type (C) which begins with a B-like pattern but is carried out with a continuous series of dewlap-coordinated repetitious head bobs, and a fourth type (D) that uses the B-like pattern but affixes 4-legged pushups to it.

A multiple display repertoire is not restricted to Anolis. Phenacosaurus heterodermus has also been found to have two distinct display patterns (Fig. 3) which appear to function differently in the same manner outlined above for anoles with A and B sized repertoires (Jenssen, 1975, Herpetologica 31: 48-58). A study of Sceloporus undulatus hyacinthinus (Rothblum and Jenssen, 1977, in press, An. Behav.) has shown this species also has more than one display pattern

(Fig. 4). The A display is shared by members of the population, is extremely consistent (strong intrapopulational stereotypy), and serves as the species' signature display. It is subject to modifiers (e.g. gorged throat, side flattening, and exaggerated limb extension of varying amplitude) to produce the "assertion-challenge" gradation in display elaboration described by Carpenter. However, these lizards also have a second pattern (B) which is similar to the A display, yet is stereotyped for the individual: each lizard's B display is unique to itself (possibly conveying individual recognition). This is in contrast to the A display which is almost identical between lizards. The B display has only been seen in high arousal contexts, predictably being performed after an A display, and may indicate increased agonistic intent. It is conceivable that iguanids in general may have a more varied signal repertoire than previously suspected.

3. Relative display stereotypy. Almost all lizards studied have display patterns which are quite predictable in form. However, these patterns are always subject to a certain degree of variability. For instance, there is inter-display variation in amplitude movements (though bob amplitudes within displays retain a stereotyped relation between bobs of a display). The temporal duration of the same display type also may show a good deal of variability (i.e. some displays are fast, others slower).

However, in some species, display durations can reflect an incredible degree of stereotypy. This temporal stereotypy may be population-wide (e.g. intrapopulation stereotypy of S. undulatus signature display), where display durations are almost the same for all lizards. The stereotypy can be on an individual level (e.g. intra-individual temporal stereotypy of A. nebulosus signature display), where display durations are constant for individuals, but vary much more widely between individuals (Jenssen, 1971, Copeia 1971: 197-209). Alternatively, the range of duration variability may also be shared by all members of the population, being as great intra-individually as that observed between the members of a population (e.g. intra-population variability of A. limifrons signature display, Jenssen and Hover, 1976, Behaviour 57: 227-240). Variation in display times may serve as an information cue. Intra-population stereotypy favors species recognition. Intra-individual stereotypy may convey individual recognition, while intra-population variability can project relative level of arousal.

4. Pattern variability. Though limited variability may exist within a stereotyped display pattern for any measured display aspect (e.g. unit duration , bob amplitude), pattern integrity almost always remains because individual movements and pauses within a display are distinct and their sequencing is constant. There is, however, one species, Anolis opalinus, whose display variability is so great that the pattern seems to have broken down (Jenssen, MS).

An elaborate computer-assisted analysis has been performed on 639 displays from 51 opalinus males representing five localities in Jamaica (Kingston and Hellshire Hills in the east, Mandeville in the middle, and Crawford by Black

River and Montego Bay in the west). The results show A. opalinus has no discrete display pattern, although there may once have been one.

The observed displays vary from 4-11 head bobs which are all of the same kind of motion consisting of a quick (0.2-0.3 s) up and down movement without any pause at the top of the bob. At the end of a bobbing sequence can be 0-8 dewlap pulses of indeterminate durations. The distribution of displays on the basis of bob number is normal (4- and 11-bob displays being rare and 7-bob displays common), and the distribution of displays according to number of dewlap pulses is poisson (0-1 pulses common and 2-7 pulses increasingly less frequent); though a particular lizard may perform displays of varing bob numbers, lizards from the western localities tend to perform more bobs per display than those from the middle and eastern localities.

A theme did emerge from the data; it suggested a set of conditions which explained about 75% of the displays. Three definite bob series are recognizable in each display having eight or more bobs. These three series are reflected in the 4-7 bob displays. The three series are: (1) an initial double bob; (2) a middle bob series in which the pauses between bobbing sequentially decrease; and (3) a concluding series in which the pauses between bobbing sequentially increase. This is idealized in Figure 5, with the actual data appearing in Figure 6. The middle series never contains more bobs than a particular display's concluding bob series. The 25% of residue displays which did not fit these conditions usually deviated by the length of only one inter-bob duration.

Most definitely, the data do not represent several discrete display patterns; there are far too many intermediates existing between any number of possible patterns to hold this point of view. My present opinion is that A. opalinus in its past history may have had two stereotyped display patterns of seven bobs each. Seven bobs is suggested by the modal number of bobs performed by most populations studied. That the early opalinus repertoire may have contained two discrete patterns comes from two observations. First, there are two highly variable patterns which appear in 6-, 7-, 8-, and 10-bob displays (Figs. 5 and 6), and second, both A. grahami and A. garmani, near relatives of A. opalinus, have two display types in their repertoires (Fig. 2).

For some reason selection pressure for display specificity relaxed; possibly during mate selection, females may have switched from using display patterning as a criterion for mate selection to some other male phenotypic feature. Anolis opalinus is the smallest of Jamaican anoles and is morphologically distinct from its Jamaican congeners. Body morphology and coloration may be a prime cue.

Anolis opalinus may hold some genetic peculiarities which are reflected by its karyotype and blood proteins. Perhaps William Hall or George Gorman would be interested in examining some individuals from populations of eastern and western Jamaica.

5. Heritability of display patterns. Determining the extent to which the genotype contributes to display patterns is beyond the scope of my research, but some indication of genetic control is indicated by display characteristics in hybrids and in sibling species. The signature display of an Anolis lineatopus neckeri X Anolis grahami hybrid was very close to its grahami parent, and quite different from the signature display of A. l. neckeri (Fig. 6). While the hybrid's signature display qualitatively resembled the grahami DAP, hybrid display duration was shorter and three times as variable as that of grahami (Jenssen, Copeia 1977: 270-276).

Of interest is that there were no signs of intraspecific aggression between the adult male hybrid and males of its parental species when paired in an enclosure. Besides the usual interspecific dewlapping and a few signature displays, no territorial defensive behavior was observed, even though the hybrid was as large or larger than the introduced males. Such confrontations between conspecific males result in strong agonistic behavior, including much displaying. The hybrid did not react as if it were a member of either parental species.

Similarity of signature displays is seen in the sibling species complex of Anolis brevirostris. Webster and Burns (1973, Evolution 27: 368-377) differentiated the species on the basis of protein characteristics and dewlap color; they recognized three sibling species distributed along the west coast of Haiti (A in the north to C in the south). I am in the process of analyzing the display repertoires of species A, B, and C, and have found that the signature display of each species is interspecifically similar (Fig. 7). Species A and C are the most similar, while comparison of adjacent species (i.e., A to B and B to C) have the greatest differences in display characteristics (Table 1).

6. Evolution of displays. This is a very speculative topic. However, indirect evidence can be obtained through the comparative method, and the brevirostris sibling species may well provide some good evidence on recently evolved differences in sibling species repertoires.

I expected to find larger differences between the signature displays of the three brevirostris siblings than I have found to date. In work with other anoles, the signature display has been the display pattern performed by males during courtship along with shallow, rapid head bobs. Theoretically, if there is a behavioral isolating mechanism based on female selection of the males' display pattern, the signature display would be most likely to show significant differences between adjacent brevirostris species. However, to my eye, at least, interspecific display differences in signature displays are subtle and dewlap color is the sharpest distinction between brevirostris taxa.

Field observation last summer and lab-controlled experiments this winter, however, have shown the males also use a seemingly more agonistic display pattern along with the signature display pattern during courtship. These displays are moderately stereotyped and appear species-unique, with quite

noticeable interspecific differences (Fig. 8). This is the first case in which I have seen the elaborate display types used in high arousal male-male encounters make frequent appearances in the courtship context.

At present, therefore, it appears that the displays that have diverged the most in these sibling species repertoires have not been the signature displays as I would have predicted. Instead, the more elaborate displays used during challenge contexts show the greatest interspecific differences. These displays are not performed by the males during the assertion context (hence are not signature displays), but do appear with rapid head bobbing and signature displays as a common behavior during courtship. This class of agonistic-courtship related displays also makes greater use of the dewlap. If dewlap color is important in sibling species recognition, perhaps dewlap color in mate selection was the selecting factor to increase interspecific differences in the agonistic displays and increase their frequence of appearance during courtship.

Table 1. Comparison of certain signature display characteristics found in the three sibling species of the Anolis brevirostris complex.

Display Characters	Species A	Species B	Species C
Number of bobs	6 - 7	5 - 7 Usually 6	5 - 7 Usually 6
Number of dewlap pulses	Usually 1	Usually 2	Usually none
Presence of tail lifts during first dewlap pulse	no	yes	no
Bob number after which longest interbob period follows	3	2	3
Ratio of first bob duration/second bob duration	About 1	Less than 1	About 1

Figure Legends

Fig. 1. Display repertoire of Anolis limifrons males constructed from an analysis of 666 displays by 23 lizards. Upper block of each figure indicates head amplitude through time and lower block shows dewlap extension through time. Black areas denote display components always present, and grey areas are variable in appearance.

Fig. 2. Comparison of the type A and B displays in the repertoires of Anolis limifrons, Anolis townsendi, Anolis grahami, and Anolis garmani. Black areas denote display components always present, and dotted lines represent variable components.

Fig. 3. Type A and B displays of a male Phenacosaurus heterodermus. Unit durations and head amplitude movements are mean values.

Fig. 4a. The type A display of Sceloporus undulatus hyacinthinus constructed from 98 displays of 11 males. Unit durations are mean values with their standard errors (white blocks) and 99% confidence limits (outer ends of black blocks) provided below the graph.

Fig. 4b. The type B displays of 79 male Sceloporus undulatus hyacinthinus showing some of the individual-unique patterns for males 7-11, and the pooled pattern (P) for six other males whose patterns were somewhat similar. Blocks under graph provide unit duration means (vertical line), standard error of the means (ends of white blocks), and 99% confidence limits of the means (ends of the outer black blocks).

Fig. 5. Hypothetical bob patterns for Anolis opalinus displays predicting the number (see parentheses) and arrangement of bobs into three series of bobs for each bob-number category. Dotted lines separate bob series.

Fig. 6. Actual distributions of bobs within each bob-number category which conform to the predicted bob patterns of Fig. 5. Total sample size (see parentheses) and number of displays explained by the predicted patterns are given for each bob-number category. Vertical lines indicate IBP means and horizontal lines provide one standard deviation either side of the mean values. IBPs are expressed as per cent of total display duration in which they appeared.

Fig. 7. Signature displays of Anolis grahami, grahami-neckeri hybrid, and Anolis lineatopus neckeri. Grey area denotes a behavior not always associated with the display. Dewlapping which can follow the head bobbing is not represented.

Fig. 8. Specific examples of signature displays from the three sibling species of Anolis brevirostris.

Fig. 9. Specific examples of more elaborate display patterns in the repertoires of the three sibling species of Anolis brevirostris.

FIG. 1

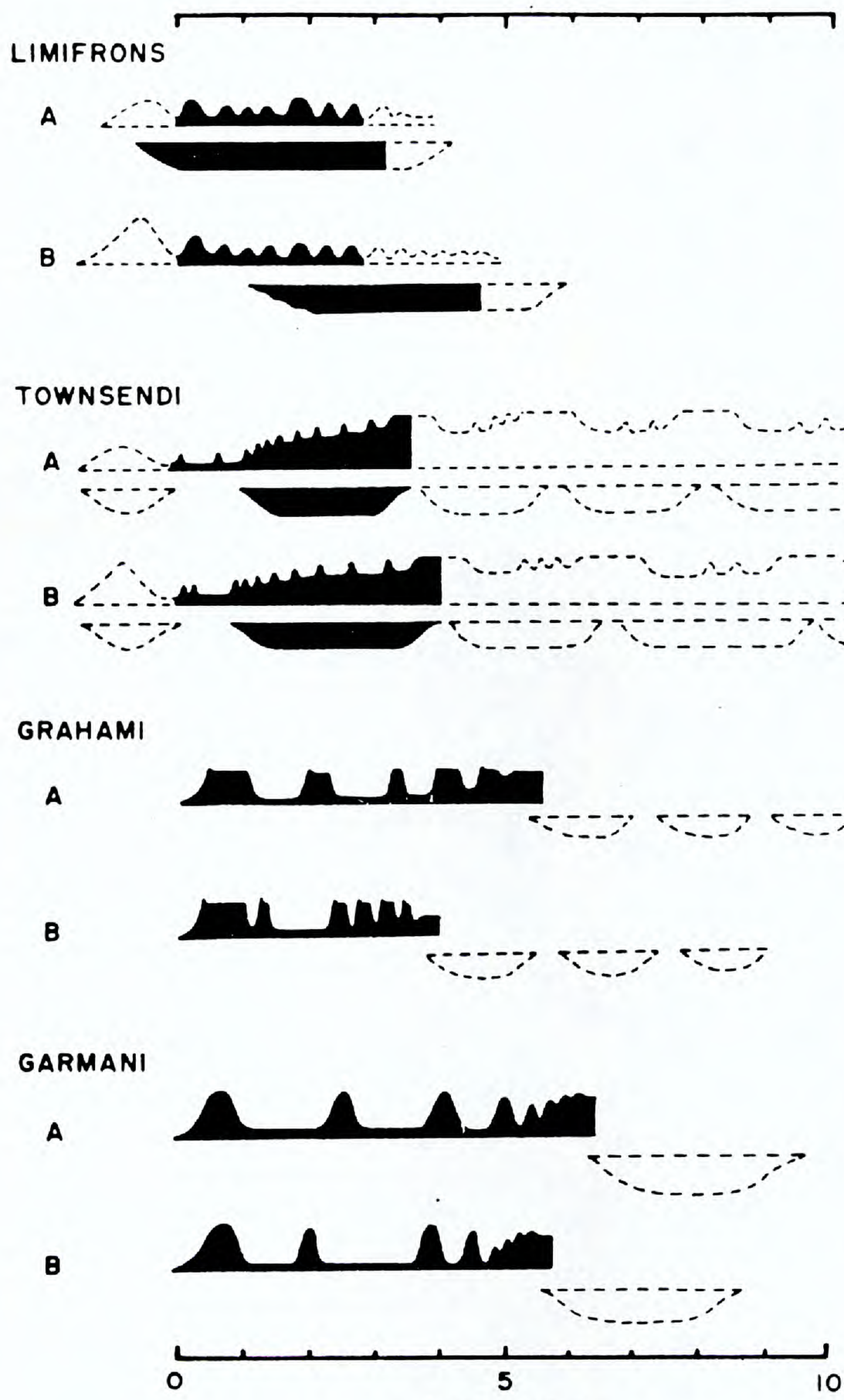
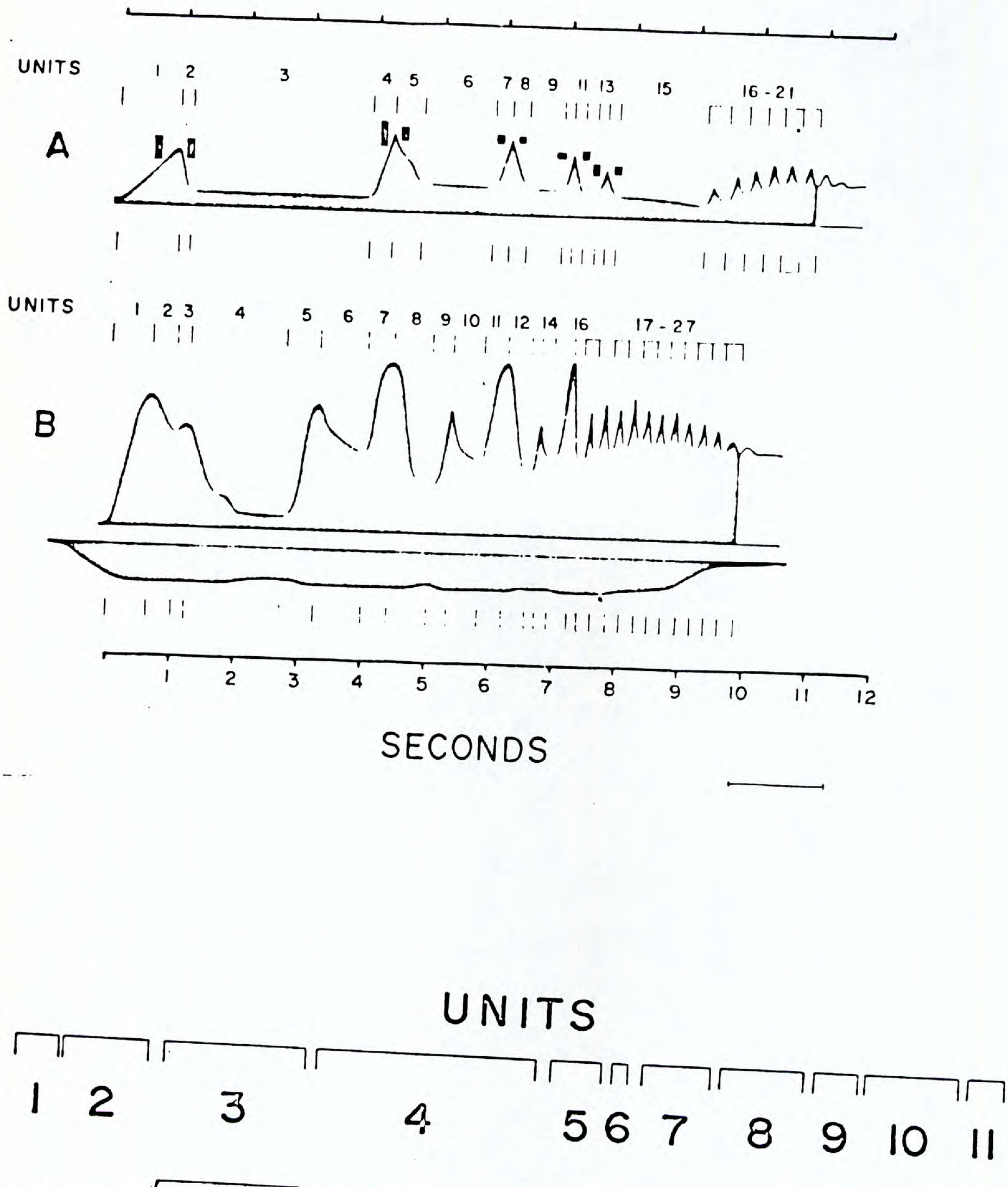

LIMIFRONS
A
B
TOWNSENDI
A
B
GRAHAMI
A
B
GARMANI
A
B
0
5
10
SECONDS

FIG. 2

FIG. 3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SECONDS

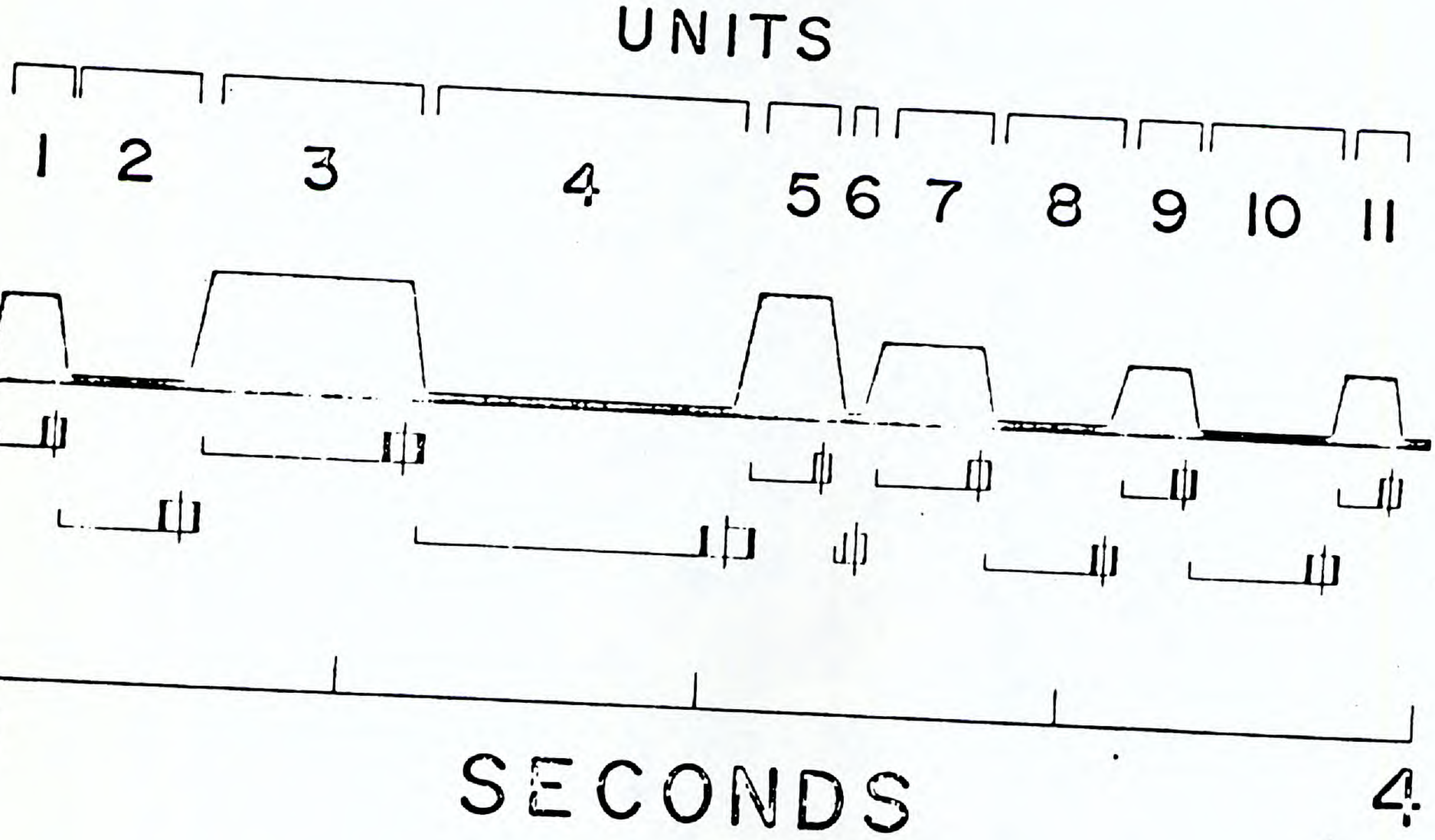
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FIG. 4a

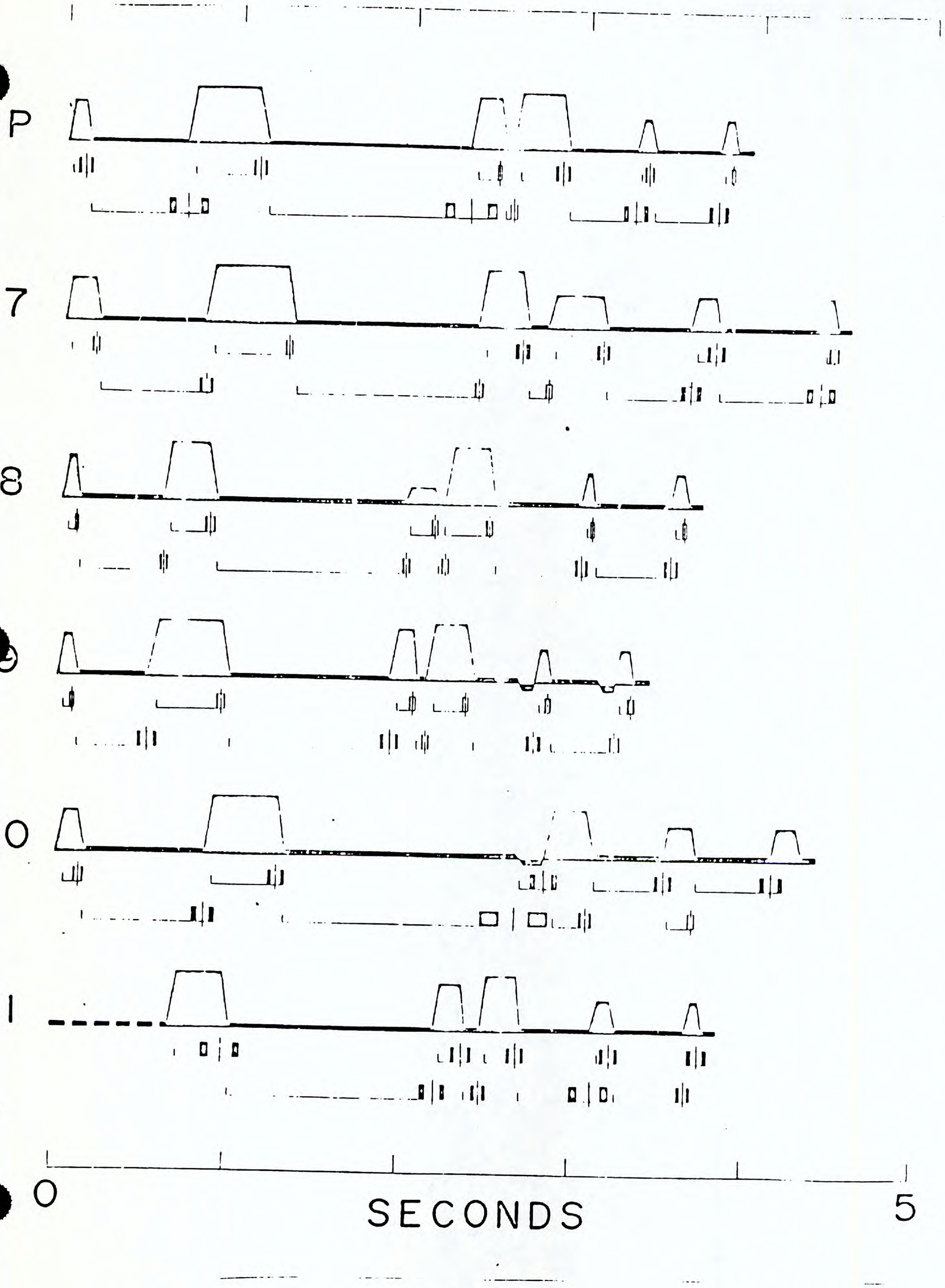
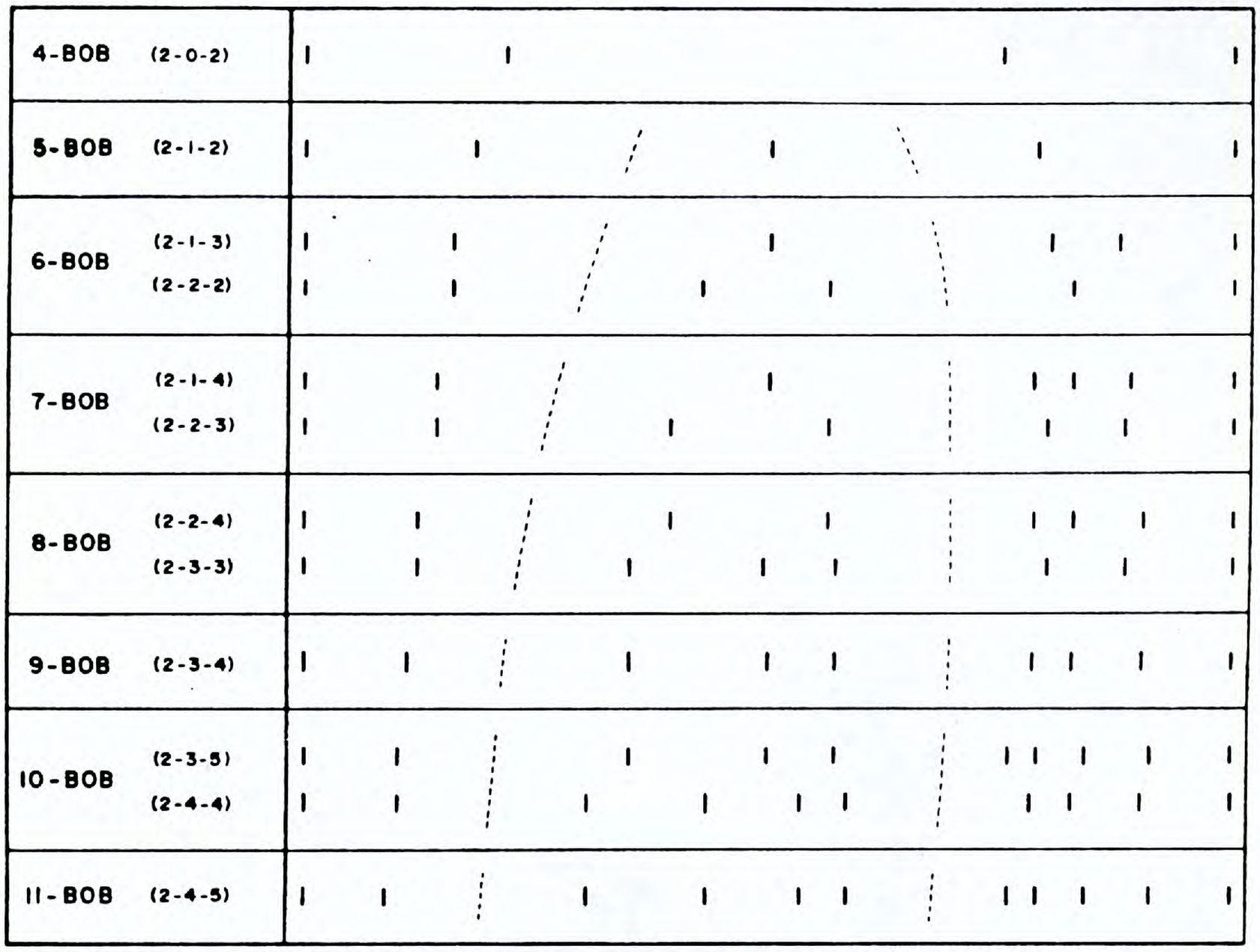


FIG. 4b

FIG. 5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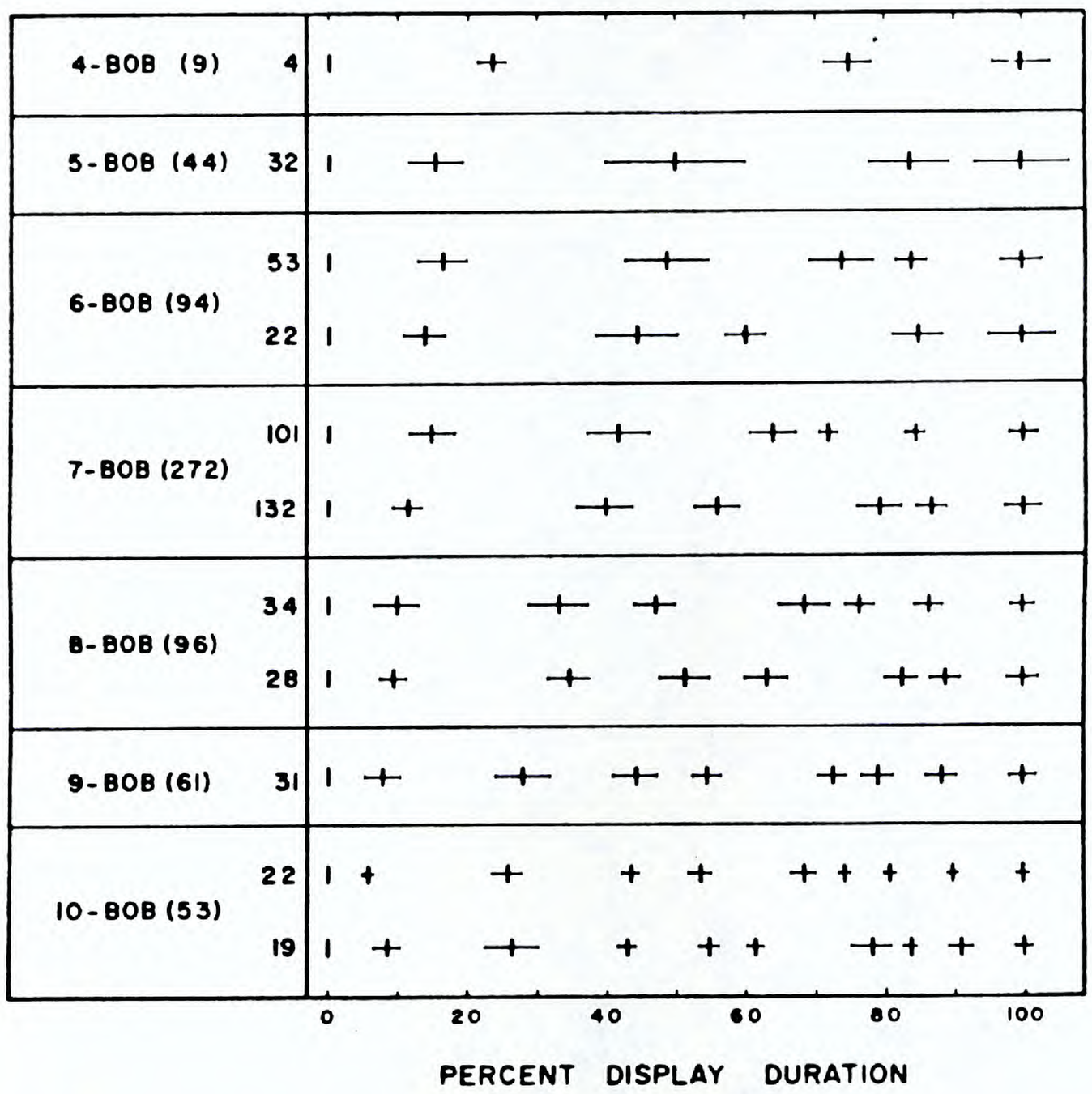
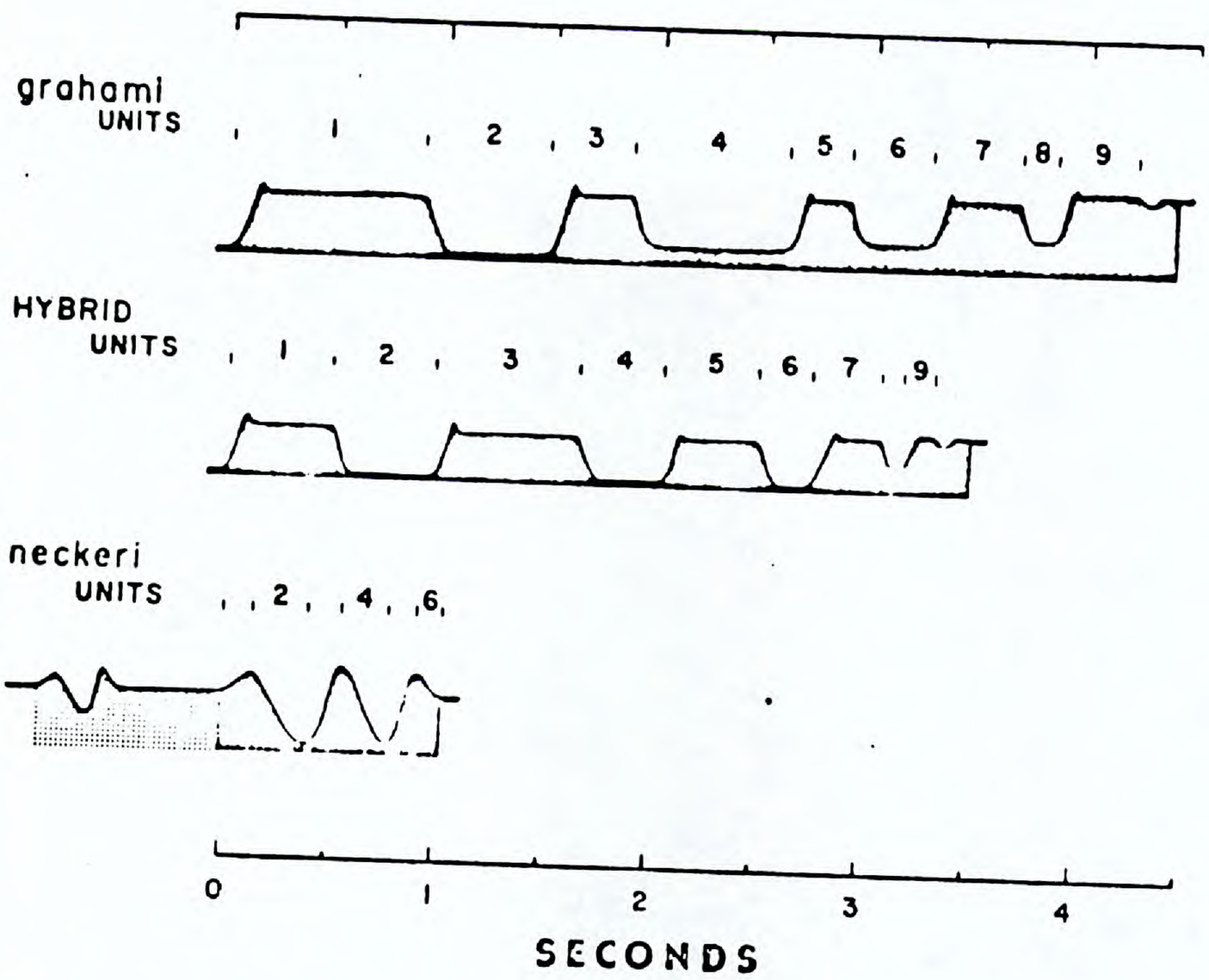
5-BOB (2-1-2)
6-BOB (2-1-3) (2-2-2)
7-BOB (2-1-4) (2-2-3)
8-BOB (2-2-4) (2-3-3)
9-BOB (2-3-4)
10-BOB (2-3-5) (2-4-4)
11-BOB (2-4-5)
DISPLAY DURATION


4-BOB (9) 4
5-BOB (44) 32
6-BOB (94) 53 22
7-BOB (272) 101 132
8-BOB (96) 34 28
9-BOB (61) 31
10-BOB (53) 22 19
0 20 40 60 80 100
PERCENT DISPLAY DURATION


grahami
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neckeri
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SECONDS

FIG. 7

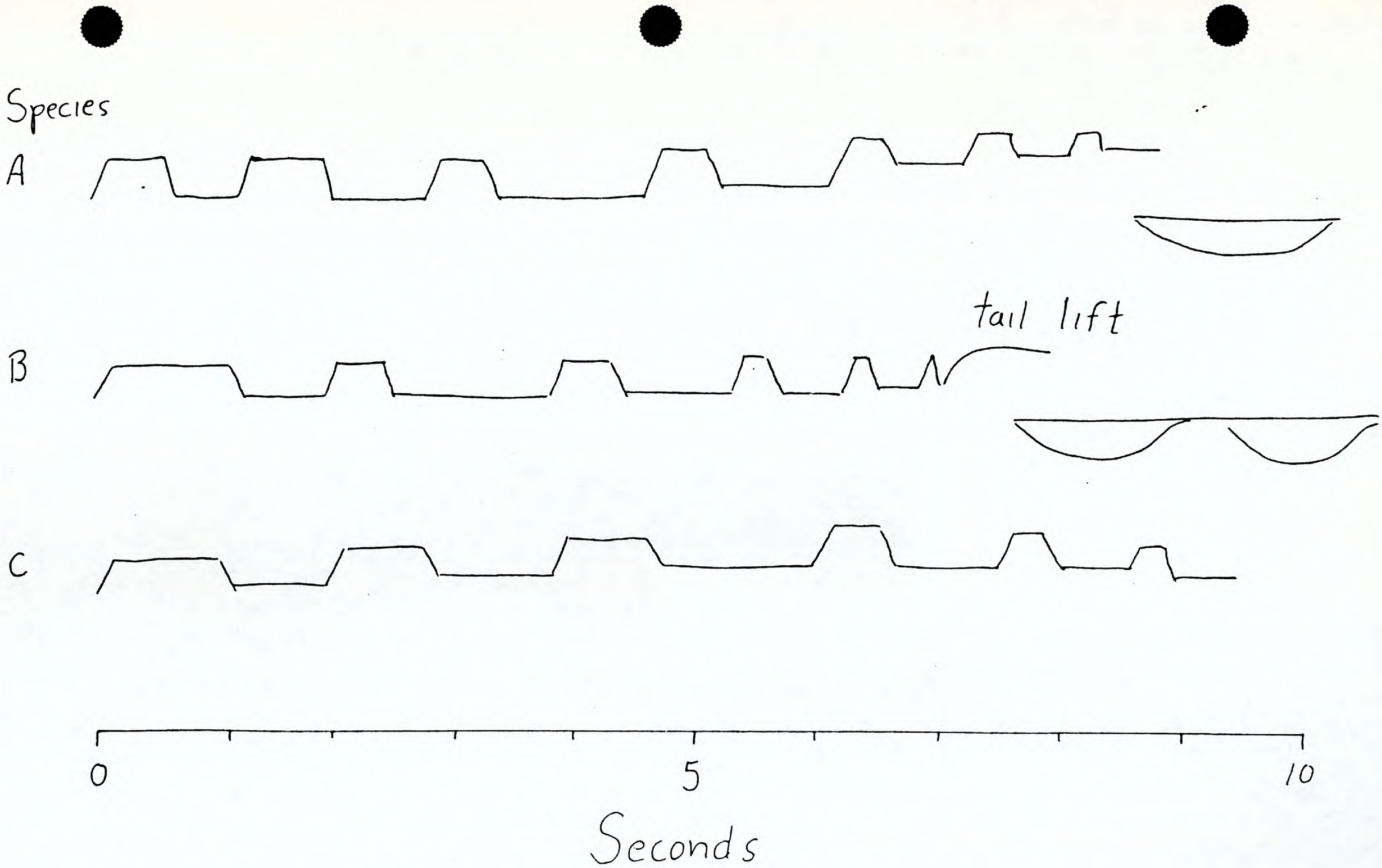


FIG. 8

Figs. 8 and 9 are deliberately left as sketches rather than finished drawings to emphasize that recording and analysis of brevirostris group displays still tentative.

Species

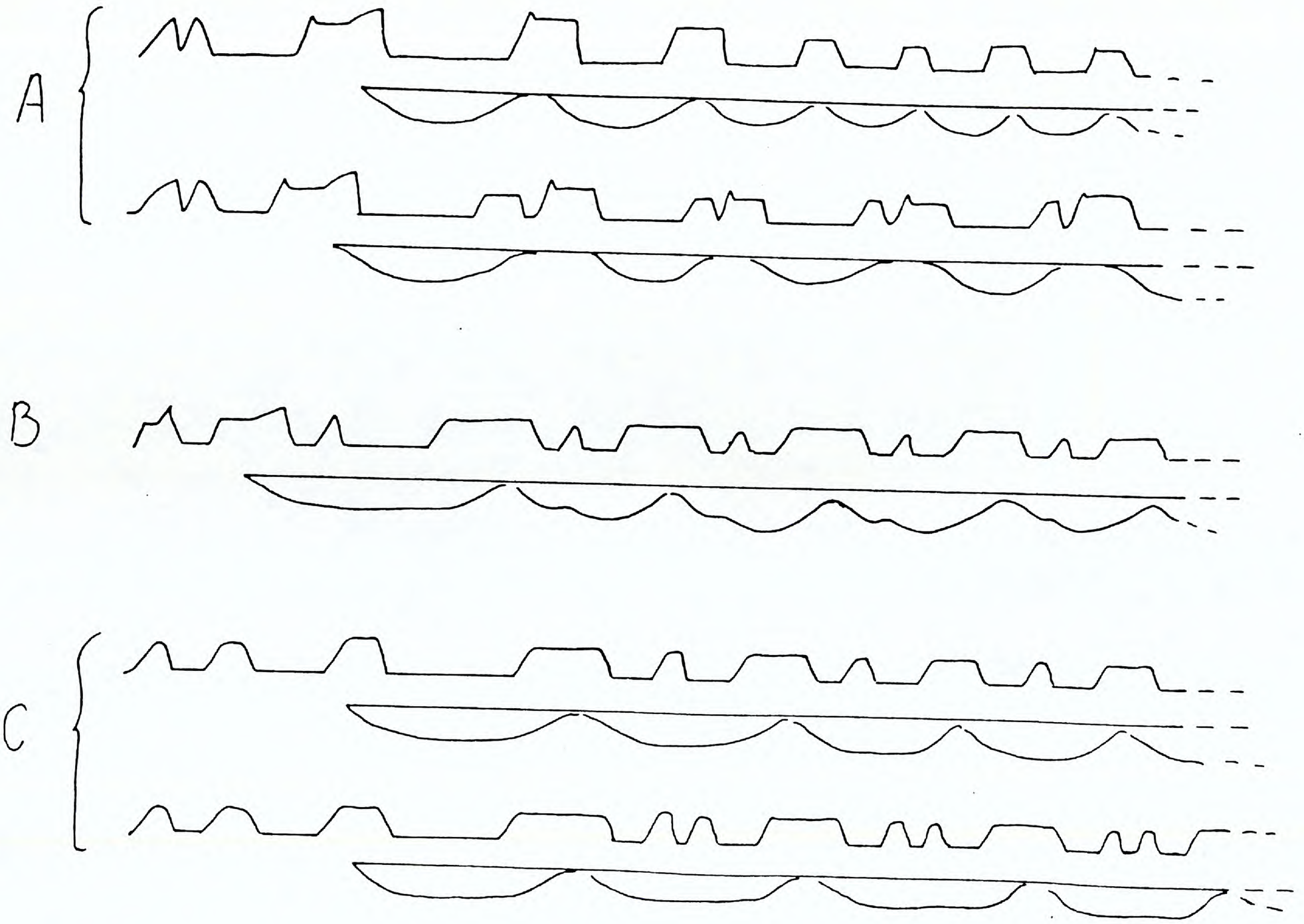


FIG. 9

A. ROSS KIESTER (University of Chicago) summarizes the work to date on Anolis onca on the Paraguana Peninsula of Venezuela, primarily by himself and Kenneth Miyata.

Harvard field parties visited the Paraguana Peninsula first in November, 1972 and then again in August, 1973. The resulting data on Anolis onca were reported by Williams (1974) in connection with a general evolutionary and phylogenetic discussion of the species. Some additional data were provided by K. Miyata in the Second Anolis Newsletter.

A more detailed study was begun by A. R. Kiester and K. Miyata in June, 1974. They selected a site on the Istmo de Medanos of the Paraguana Peninsula about 10 km north of the town of Coro. (Miyata had watched onca here in 1973.)

The site is a small "island" of high ground surrounded by mudflats which show signs of being occasionally under water although they have been dry during all of their visits. The island is about three acres in areas and was christened "Anole Atoll." The island is about 50 m from the center of the isthmus which constitutes continuous habitat for the lizard.

In June, 1974 the vegetation of the island was mapped and as many lizards as possible were marked. The marked lizards were followed through July first by Kiester and Miyata and then by R. Leuthueser. Kiester returned in September of 1974 and again in March of 1976 with J. Walters and D. Rabinowitz. Data from these three visits plus some data from the two earlier visits are now being worked up into a report on the ecology and natural history of this species. Here we summarize the findings and comment upon them.

Habitat and Habitat Use. Vegetation on the island consists primarily of widely scattered acacia bushes and opuntia with varying amounts of a small shrub and some grass. The acacias are small and range in size up to about 4 ft. high and perhaps 10 ft. across. Many are essentially bare of leaves. The opuntias are mostly small. The lizards generally live on the acacia bushes which have thick patches of grass growing at the base. In the course of over 100 hours of observation about 775 spot observations were made on the perches used by marked individuals. The anoles are usually perched on the thorny stems of the bushes, most often near the base. Sometimes they are found on the grass at the base of the bushes or on an opuntia. They were rarely seen in the windswept green tops of the bushes. This was in contrast to the nearby continuous stretches of habitat where, at least at some times, the lizards were frequently perched in the dense spiny tops of the low bushes.

The daily cycle of activity for this species shows a peak of activity in midmorning, lower activity during the hottest part of the day, but a marked decrease in the number of lizards seen from about 1500 until dark. Since most individuals seen during this later period are still perched on the shaded windward side of the bushes, and very few are perched on the sunny lee side, it must be more important for them to face the wind than to maintain an elevated body temperature at this time of day. Some individuals, usually adult

males, are found both in the sun and wind during this period, perched on small clumps of cactus which provide no wind barrier, or wandering about on the ground near their home bush. In June, July and September, smaller lizards and females were almost never seen on the ground. In March, several juveniles were seen out on the ground. At any one time only a fraction of the population was visible. Usually a majority of the lizards were (presumably) hiding inside the grass at the base of the bushes during any one census of the island.

Thermal Relations. Over 80 body temperatures were recorded for animals both on the island and on the nearby mainland. Analysis of 106 sample body temperatures regressed against air temperature yielded a value of $k = .875$. This k is the measure of the precision of thermoregulation of Huey and Slatkin (1976). A value of k very close to unity, as this one is, indicates that this species is not thermoregulating at all, at least while they are active. Thermoregulation is probably very difficult for this species because of the action of the wind which tends to bring the lizards into thermal equilibrium with the air very quickly (the opposite of the wind chill factor).

Home Range. Home ranges tend to be quite small; with some exceptions individuals did not leave the vicinity of a given bush. The number of lizards per bush or continuous clump of bushes varied according to the extent and complexity of the vegetation structure, with up to six individuals using the same patch. Some individuals were observed to move from one bush to another. Sometimes an individual would show up at several different bushes and then disappear, while others would move to an adjacent bush for a few days and then return to the bush where it was first seen.

Social Behavior. Adult males vigorously react to the presence of intruder males placed in the territory on a tether. Each bush or clump of bushes had only one full grown male (although it may have had a smaller male or two). Natural social interactions were observed between full grown adult males on a few occasions. These encounters in March, June, July and September took place in the late afternoon and were on the open ground between two bushes. They consisted of much vigorous headbobbing and dewlapping and some chasing and biting. It is therefore quite likely that the full grown adult males are territorial in a very classical fashion. Females also react to tethered intruders, but apparently less vigorously. Social interactions are much more common in November.

Feeding and Food. Few instances of food capture were noted, but those that were seen involved a lizard moving from a low perch onto the ground to pick up an item, or feeding by individuals who were already on the ground. The first behaved like classical trunk-ground sit-and-wait foragers (except that they were on small branches rather than trunks). However, two observations of prey capture by adult males out on the ground in the afternoon showed the existence of a striking prey-stalking behavior. The prey in these cases were robber flies and the lizards moved towards them very carefully using irregularities in the ground as cover when stopping. Finally they would dash at the fly from the last stopping point. This type of stalking behavior is not like that of,

say, Cnemidophorus or Ameiva but is rather more like that of a cat. This behavior pattern needs to be documented more fully, but appears to represent an example of a prey capture tactic not previously noted for the genus. The observations suggest that the repertoire of prey stalking tactics may be broader than previously supposed and that the expression of prey stalking tactics may depend on the ecological circumstances. Few other species of anoles ever forage on open flat ground.

Based on our present limited knowledge, Anolis onca appears to subsist primarily on invertebrates. Richard Salvato has analyzed a series of 38 stomachs from a variety of localities and the results are presented in Table 1. A single species of chrysomelid beetle made up a large portion of the stomach contents in the animals in which it was present. In addition to the arthropods, Salvato found a snail and shed skin. He also has an observation of an onca in the process of swallowing a female Cnemidophorus lemniscatus.

Kiester believes that it may be possible that the "island" population of onca may be acting essentially as aeolian planktivores because the sparse vegetation may produce little food and the strong winds may blow in significant amounts of insect prey. Clearly what is needed to substantiate this belief are stomach contents of island lizards and measurements of insect density on the island and of the amount of potential food blown in by the wind.

Size, Growth, and Reproduction.

Although our data is mixed from two different years and thus is not wholly reliable, a plot of the size distribution of the lizards for the three different times of the year that we have visited the island is interesting (Figs. 1 and 2). From these figures we can see that mean body size increases through the year. Further, the variance in body size decreases. That is, the population grows up until most all of the members are of adult size and there are no young in September. From this pattern and the fact that (according to local residents) rainfall occurs principally in December and January, we may infer that reproduction is very seasonal. A likely hypothesis is that eggs are formed and laid after the first rains so that the young come out in January and February (and possibly March). These young plus those lizards left from the previous year then grow throughout the rest of the year. By September most of the lizards in the population are adults and this situation continues until the next rainy season.

Another aspect of the annual variation in size patterns is the extreme sexual dimorphism in size. Females are never larger than 68 mm SV while males can grow up to 89 mm SV. In September females are restricted to a narrow size range of 59-69 mm while males range from 58-89 mm. There is a peak in the distribution of males at 64 mm which is the average size of females at that time. Males above the maximum female size of 68 mm are more evenly distributed as to size. The occurrence of a group of female-sized males at this time is suggestive. It seems to be the case that these smaller males may be tolerated

within the territory of an adult sized male while we know that large adult males never tolerate each other. This raises the intriguing question as to whether there is some control over the growth of males either though some social effect or through direct competition for food in which the larger male usually wins. It may be that smaller males who cannot get their own territory are in some way forced to remain at female size until they can strike out on their own. If such a "gating" phenomenon is occurring, it needs to be carefully documented and the elucidation of the mechanism will prove to have important implications for the nature or the relationships of growth, competition, and social systems in this species.

Survivorship. Of 55 animals marked in June and early July, 1974, a total of 26 were recaptured in September after an interval of at least 80 days (Table 1). Upon return to the island in March of 1976, over 18 months later, no lizards could be confidently identified as having been marked before, although two were possibilities. We have some indication that they may be able to regenerate toes. In any event, the data from 1974 alone show a lower rate of disappearance than is found for most mainland anoles. This may reflect lower mortality rates, although it may be due to lower emigration rates as well.

Predation. Predation seems very low for the lizards on the island. The only bird predator observed on the isthmus that could conceivably catch A. onca is the caracara, but these seem to have too much trouble maneuvering in the wind to be a threat. The mockingbird (Minus gilvus), which nested on the island, may take juveniles. On the main part of the isthmus several individuals of the large colubrid, Mastigodryas pleei were seen foraging. These probably take A. onca, but none were ever seen on the island itself.

Movement On and Off the Island. Our original impression was that there would be relatively little movement on or off the island because of the hostility of the intervening mudflat environment. However, in March when numbers of small individuals were seen, we saw a number of these smaller lizards out on the edge of the island and in one case found a small juvenile some 20 m out into the mudflats. Thus dispersal between the islands and to and from the mainland may be greater than we had previously expected.

Summary. Anolis onca clearly represents an extreme in Anolis habitat preference. Windborne food and low predation rates appear to go along with this habitat. Both of these factors are associated with the wind, and as Williams has remarked, the wind seems to be the key to the ability of this species to live along the coastal desert, and the lack of wind anywhere except right along the coast appears to explain the absence of the species further inland.

Our study area has now been followed for three calendar years and during our last visit the individual bushes mapped in the study were marked permanently using aluminum tree tags. Because of the location of the study area, we feel confident that it will not be disturbed by human activities. We hope that the site will remain useful for many years to come.

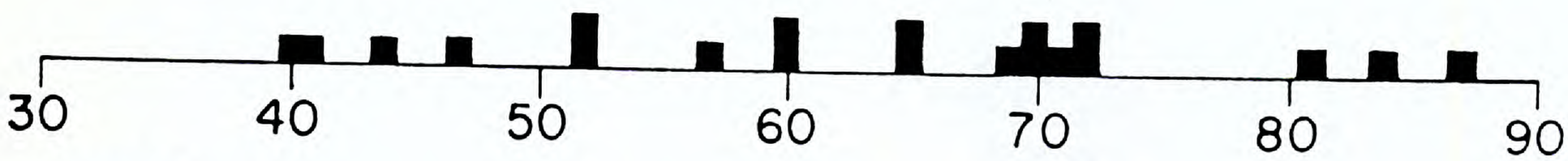
TABLE 1

	Number present In June	Number present in September	Percent remaining
females	25	14	56
males	30	12	40
Total	55	26	47.3

Disappearance rate of marked Anolis onca on Anole Atoll. A minimum of 81 days between June and September observations. Twenty-two of these animals were seen after intervals of 95 days.

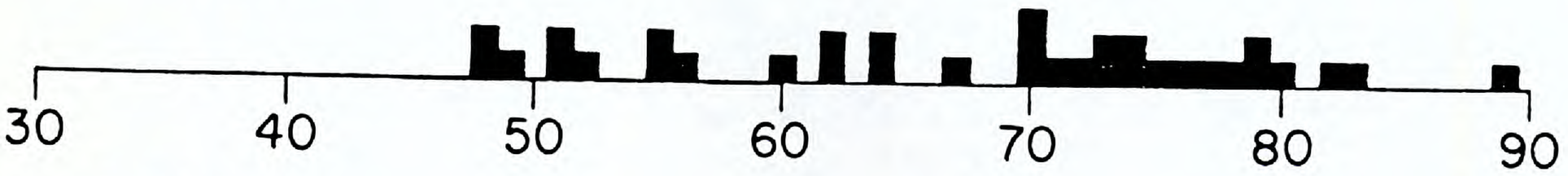
N = 20
$\bar{X}$ = 62.95
S_X = 13.83
$S_{\bar{X}}$ = 3.09

MARCH 1975



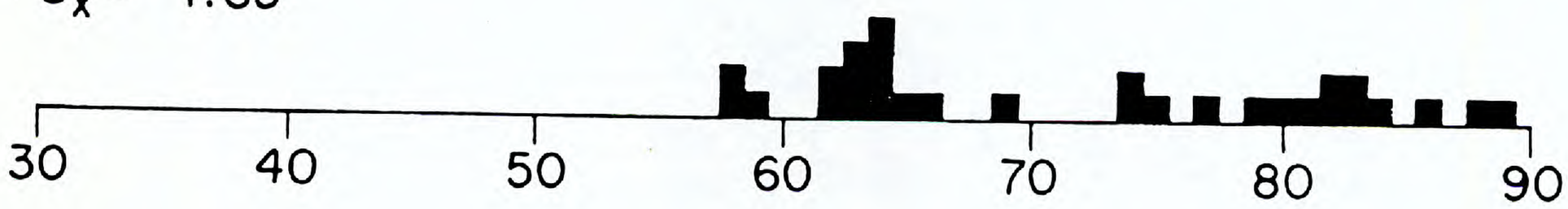
N = 34
$\bar{X}$ = 66.76
S_X = 11.02
$S_{\bar{X}}$ = 1.89

JUNE – JULY 1974



N = 30
$\bar{X}$ = 72.03
S_X = 10.03
$S_{\bar{X}}$ = 1.83

SEPTEMBER 1974



MALE

FIG. 1

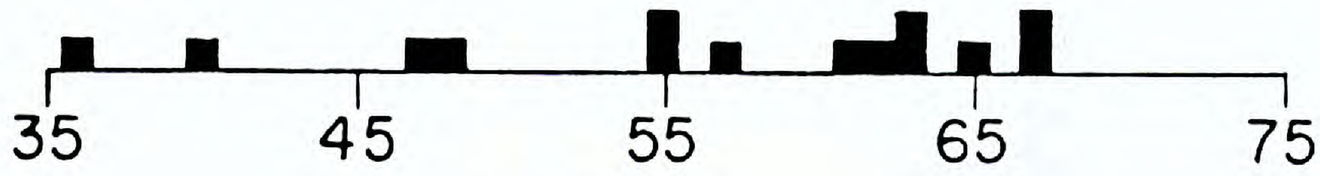
N = 14

$\bar{X}$ = 56.21

S_X = 9.79

$S_{\bar{X}}$ = 2.62

MARCH 1975



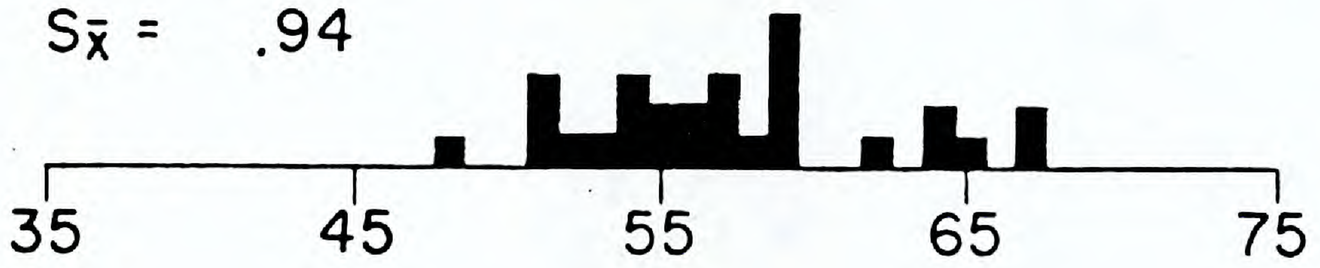
N = 28

$\bar{X}$ = 57.25

S_X = 4.99

$S_{\bar{X}}$ = .94

JUNE – JULY 1974



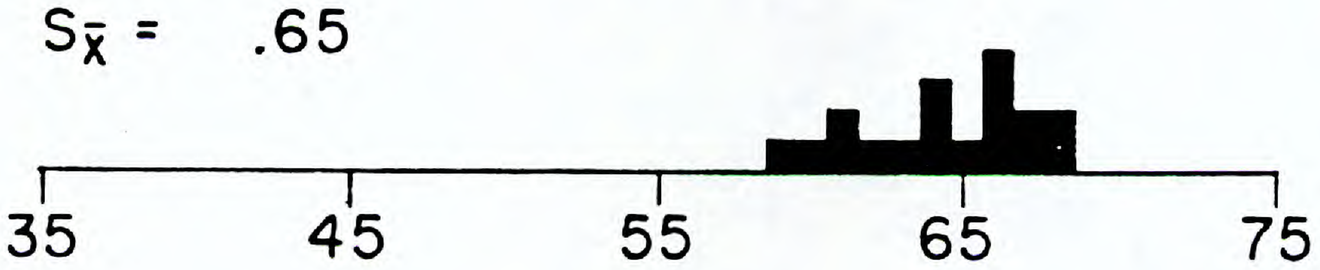
N = 18

$\bar{X}$ = 64.28

S_X = 2.76

$S_{\bar{X}}$ = .65

SEPTEMBER 1974



FEMALE

FIG. 2

Papers cited:

Huey, R. B. and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol. 51: 363-384.

Miyata, K. 1974. Report in E. E. Williams (Ed.), The Second Anolis Newsletter.

Williams, E. E. 1974. A case history in retrograde evolution: the onca lineage in anoline lizards. I. Anolis annectens, new species, intermediate between the genera Anolis and Tropidodactylus. Breviora Mus. Comp. Zool. No. 421: 1-21.

KENNETH MIYATA (graduate student, MCZ, Harvard) reports some of his Ecuadorian observations.

A. Ecological Notes on Ecuadorian anoles

1. Anolis aequatorialis Werner

This species was fairly common on the west slope of the Andes between 1350 and 1900 m on the Tandapi, Tandayapa, and Chiriboga roads. Only a single individual was seen active, however, and this was on the floor of cloud forest at 1650 m. The area was densely shaded and both body and ambient temperatures were 18.4°. All other specimens of the species were found sleeping on low vegetation in both cloud forest and along forest edges.

2. Anolis bitectus Cope

This species was found only at Hacienda "Cerro Chico," about 45 km N of Quevedo. Nearly all were found in the low understory vegetation of a rubber tree plantation, although a few were seen on the trunks of the trees as well. Population density in the plantation was calculated to be around 500/ha.

3. Anolis chloris Boulenger

This species was found in the western lowlands and the lower slopes of the Andes up to about 900 m. A fairly common lizard, it was most frequently seen above 5 m, although they are often much lower, and a few were seen on bushes. They seem to spend most of their time on the trunk or major branches, but all prey captures observed took place on leaves. Copulation was observed five times, always more than 5 m up on the trunks. With 48 body temperatures, the mean was 24.8 with the Huey-Slatkin k = .683. [1]

4. Anolis fasciatus Boulenger

This species was found in the western lowlands up to an elevation of 400 m. Although it is very rare in the virgin rain forest at Rio Palenque, it is fairly common in old cacao groves in the vicinity of Quevedo. It is most frequently seen on the trunks of fairly large trees, usually within 2 m of the ground. With 15 body temperatures, the mean was 25.0 with k = .676.

5. Anolis festae Peracca

This species was found in relatively open situations from Rio Palenque south to Machala below 200 m in elevation. They were most abundant on tree rows along the roads, which were characterized by well-spaced trees and short grassy understory. Most were within a meter of the ground, frequently 30 cm or lower, and usually hidden by the short grass at the base of the trees. With 27 body temperatures, the mean was 24.2 with k = .887.

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[1] R. B. Huey and M. Slatkin, 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol. 51: 363-384.

6. Anolis fraseri Gunther

This species was found between 800 and 1400 m on the west slope of the Andes. Two individuals seen during the day near Tinalandia were on isolated trees, one on the trunk about 2 m off the ground and the other in the crown about 9 m up. Another was found sleeping on a tree fern about 3 m tall in cloud forest at 1400 m elevation. A single body temperature of 25.4° was recorded.

7. Anolis fuscoauratus D'Orbigny

This species was seen in eastern Ecuador between 400 and 1000 m in elevation. It was most abundant in a garden in Puyo where it was most easily found sleeping at night. Most of the active lizards were seen hopping around in the lush vegetation. Several were seen on tree trunks at the edge of secondary forest near Puerto Misahaulli. None were seen in virgin forest SE of Veracruz, and they were very uncommon in secondary forest just outside Puyo.

8. Anolis gemmosus O'Shaughnessy

This species was abundant between 1300 and 1900 m on the west slope of the Andes on the Tandayapa, Tandapi, and Chiriboga roads. It was encountered as high as 2100 m. Despite their abundance, relatively few were seen active during the day. Most of the sleeping lizards were found on ferns within a meter of the ground, and many of the active ones were seen in the same places.

9. Anolis gracilipes Boulenger

This is a fairly uncommon species which was found in forest on the western slopes between 200 and 800 m in elevation. All individuals have been seen on ferns or other understory plants with a similar growth form within 1.5 m of the ground. They tend to perch on the very tips of leaves with their bodies raised high above the surface.

10. Anolis maculiventris Boulenger

Only two individuals were seen at Tinalandia in forest at an elevation of 800 m. Both were sleeping on leaves in primary forest within 1.5 m of the ground.

11. Anolis parvauritus Williams

This species was seen only at Rio Palenque, where it was quite uncommon. Most individuals were found in scrubby vegetation along the edge of undisturbed forest, although two individuals were seen high in the crowns of trees from vantage points on steep slopes. It seems likely that this is a crown species which gets within reach only where the crown itself descends near the ground.

12. Anolis peraccae Boulenger

This species was quite abundant in disturbed habitats on the western lowlands and were found as far south as Bucay and as high as 1400 m. This species is found most commonly on the trunks of small to medium-sized trees within 2 m of

the ground. It is often much higher, however, particularly in forest. It is associated with openings in the crown in forest and avoids the densely shaded interiors of cacao and rubber plantations. With 84 body temperatures, the mean is 24.7 with k = .932.

13. Anolis princeps Boulenger

This species is reasonably common in forest and forest edge situations below 200 m in western Ecuador. All individuals seen were on tree trunks within 2 m of the ground and most were obscured by thick understory vegetation. This species evidently went through a population decline at Rio Palenque between 1975 and 1976. With 8 body temperatures, the mean was 24.7° with k = 1.006.

14. Anolis sp. near lemurinus

This species has been found on the western lowlands between 150 and 800 m in elevation. It is most often seen on the trunks of medium to large trees within a meter of the ground, but individuals have also been seen in the herbaceous understory of small forest clearings and on building walls and high up on the trunks of large trees.

15. Anolis sp. (eulaemus group)

A single individual was found on the floor of dense virgin forest SE of Veracruz in eastern Ecuador, and another individual was collected in dense forest closer to Puyo by an Indian woman.

These observations are presented only as an indication of what the lizards might be doing. All of the observations were confined to the months of June, July, August, and early September, a time which corresponds to the dry season in western Ecuador. In the case of the less frequently observed species, it should be noted that there may be significant shifts in structural habitat during a single day (see Fig. 1 for such daily shifts in perch height of A. peraccae), and between different years (Fig. 2, again for A. peraccae). Local patterns of distribution can shift considerably within relatively short periods of time as well (see below).

B. Species Interactions

Table 1 shows the patterns of sympatry observed in western Ecuador over the past three years. Although there may be as many as eight species found together in broad sympatry, no more than six have been found syntopically. These figures are comparable to complex anole communities in the Greater Antilles and Central America. The major difference between the Greater Antilles and western Ecuador is in the degree of dominance and in overall population density. South American

anoles are rarely encountered in high densities, and even where they are there are rarely more than two species present in any number. All of the study sites in western Ecuador are disturbed to some degree, because it is in these habitats that populations are largest (or at least most conspicuous). In some cases it may be possible to compare forest and disturbed habitat populations of the same species, but this will require more data than is presently available.

1. Anolis peraccae-Anolis chloris

A balsa tree row study site at Centro Cientifico Rio Palenque in the western Ecuadorian lowlands has been monitored during the dry season from 1974 to 1976 (Fig. 3). In 1974 and 1975 this area could be divided into three zones: a) an area where the balsas were separated from forest by a strip of bananas and oil palm where peraccae was the only species present, b) an area where the balsas were bordered on both sides by forest and second growth where anoles were much less abundant, and c) an area where the balsas were bordered on only one side by the forest where both peraccae and chloris were found (three other species of anole were seen on the study site but they accounted for less than .65% of the total observations). By 1976, however, the situation had changed considerably (see Table 2). Between 1975 and 1976 both species evidently decreased in population, but whatever caused the decline had a more severe effect on peraccae, and chloris was able to invade a greater part of the habitat. The two species, when they do coexist, neatly divide up the vertical component of perch height (Fig. 4).

2. Anolis peraccae-Anolis festae

The balsa census site completely lacked A. festae until 1976 when two observations were made there, both on the same tree. In 1975 festae was quite abundant in similar habitat only a kilometer or so distant (Fig. 5). The most apparent difference had to do with the proximity of forest: in the guayacanes (a), festae was considerably more abundant than peraccae; in the balsas in section B, which are surrounded by cleared cultivated land, peraccae dominates but a few festae are also present, and in the balsa row in section C (which is the portion described above) festae was completely absent. The two observations of festae in 1976 are probably significant, as festae seems to be an actively expanding species moving from relatively xeric (or at least highly seasonal) habitats into the more mesic (and less seasonal) area around Rio Palenque. Peraccae and festae seem to be invading similar habitats, but from different directions.

It is not immediately clear whether the syntopy of peraccae and festae is stable. Both species are very similar in size, and data taken from syntopic populations show no significant differences in perch preferences or body temperature. In rubber groves south of Rio Palenque where both species are abundant, festae appeared to be much more restricted to the very edges of the groves than peraccae. It is not likely that differences in thermal biology would show up during the dry season, as the entire region is uniformly cloudy most of the time, but there may be differences in tolerance to desiccation of

eggs or juveniles or even adults. In the same rubber groves a third species, bitectus, is abundant, but it is almost completely restricted to understory herbs where the other two species are never found.

3. Anolis fasciatus-Anolis peraccae

This is the dominant species pair in the old cacao groves in the Quevedo area. Most of these plantations date back to the late 19th century or so, and are characterized by large shade trees, heavy growth of epiphytes, and little understory. There appears to be almost complete segregation of the two species on the basis of trunk texture and size. Peraccae is generally found only on the cacao trees themselves while fasciatus is on the smooth trunks of the much larger shade trees. There are no significant differences in body temperature of syntopic populations or in perch height.

4. Anolis gemmosus-Anolis aequatorialis

These are the dominant species in the montane forests of the western Andes. Because these species are easy to sample at night while they are asleep, most of the data were obtained in this fashion. Both species are very cryptic and relatively hard to find during the day, and the information is summarized above. In terms of relative abundances, gemmosus seems to be about four times as abundant as aequatorialis at localities between 1350 and about 1650 m. Above this gemmosus is relatively more abundant, although actually less common than at lower elevations. Recapture data seem to indicate that aequatorialis moves around considerably more than does gemmosus.

TABLE 1

	aequatorialis	biporcatus	bitectus	sp. nr. lemurinus	chloris	chrysolepis	fasciatus	festae	fraseri	fuscoauratus	gemmosus	gracilipes	maculiventris	ortoni	peraccae	princeps	punctatus	trachyderma	transversalis
aequatorialis					*				X		X		*		*				
biporcatus	X	X										X			X	X			
bitectus			X												X				
sp. nr. lemurinus	X	X	X									X	X		X	X			
chloris		X	X	X								X	X		X	X			
chrysolepis					*								*				*	*	*
fasciatus			X									X			X	X			
festae															X				
fraseri							X	X	X						X				
fuscoauratus													*				*	*	*
gemmosus												*			X				
gracilipes													X		X	X			
maculiventris															X				
ortoni																	*	*	*
peraccae													X						
princeps																			
punctatus																		*	*
trachyderma																			
transversalis																			

Sympatry in Ecuadorian Anolis. Based on observations of Miyata (X) and on recent collections (*).

TABLE 2. Population density comparisons: Anolis chloris and A. peraccae on Rio Palenque balsa study area, 1975-1976.

	1975		1976	
	n	n/hr	n	n/hr
Anolis chloris	161	4.34	163	4.26
Anolis peraccae	530	14.28	120	3.14

FIGURE CAPTIONS

Figure 1. Daily shift in perch height for Anolis peraccae at Rio Palenque balsa study area.

Figure 2. Three year shift in vertical perch distribution at Rio Palenque balsa study area.

Figure 3. Rio Palenque balsa study area, showing local distribution of A. chloris and A. peraccae in dry season of 1975.

Figure 4. Vertical perch distribution of A. peraccae and A. chloris compared. Rio Palenque balsa study area, 1974-1975 data.

Figure 5. Distribution of three common species of Anolis at Rio Palenque: 1975. Section A. A. festae most common; A. peraccae common; A. chloris apparently absent. Section B. A. peraccae most common; A. festae and A. chloris much less common. Section C. Balsa study area (see text and Fig. 3). A. festae absent.

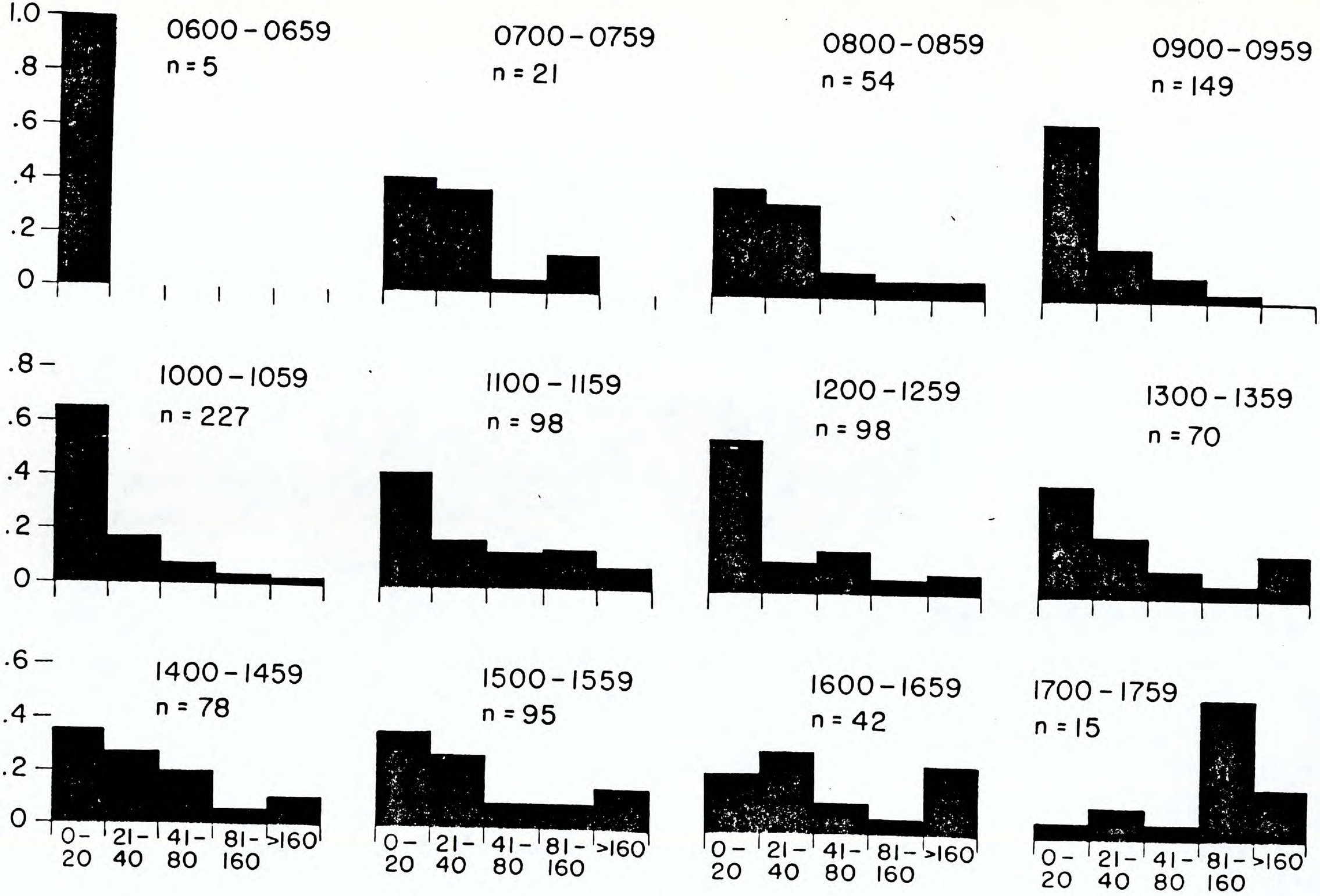
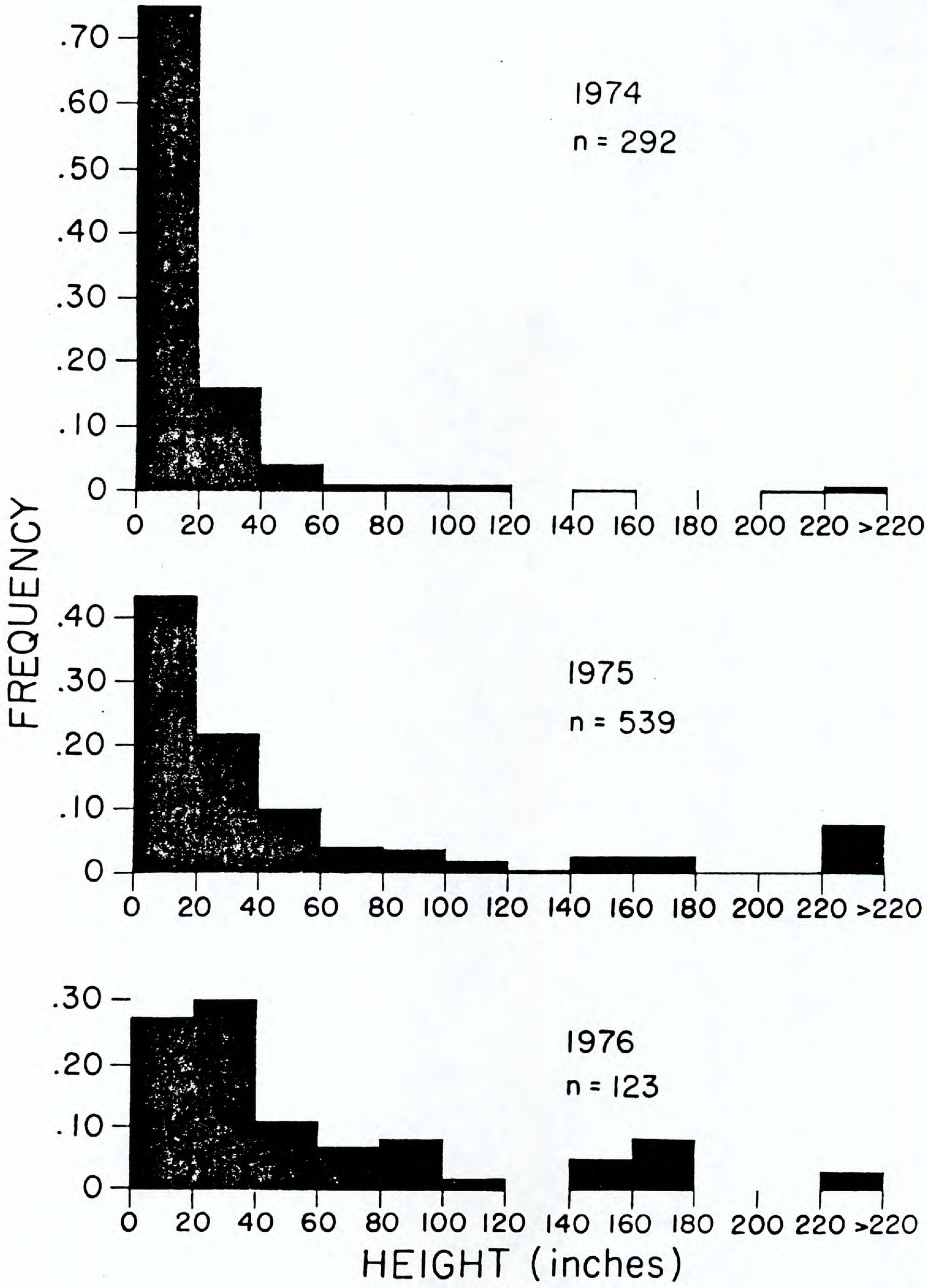
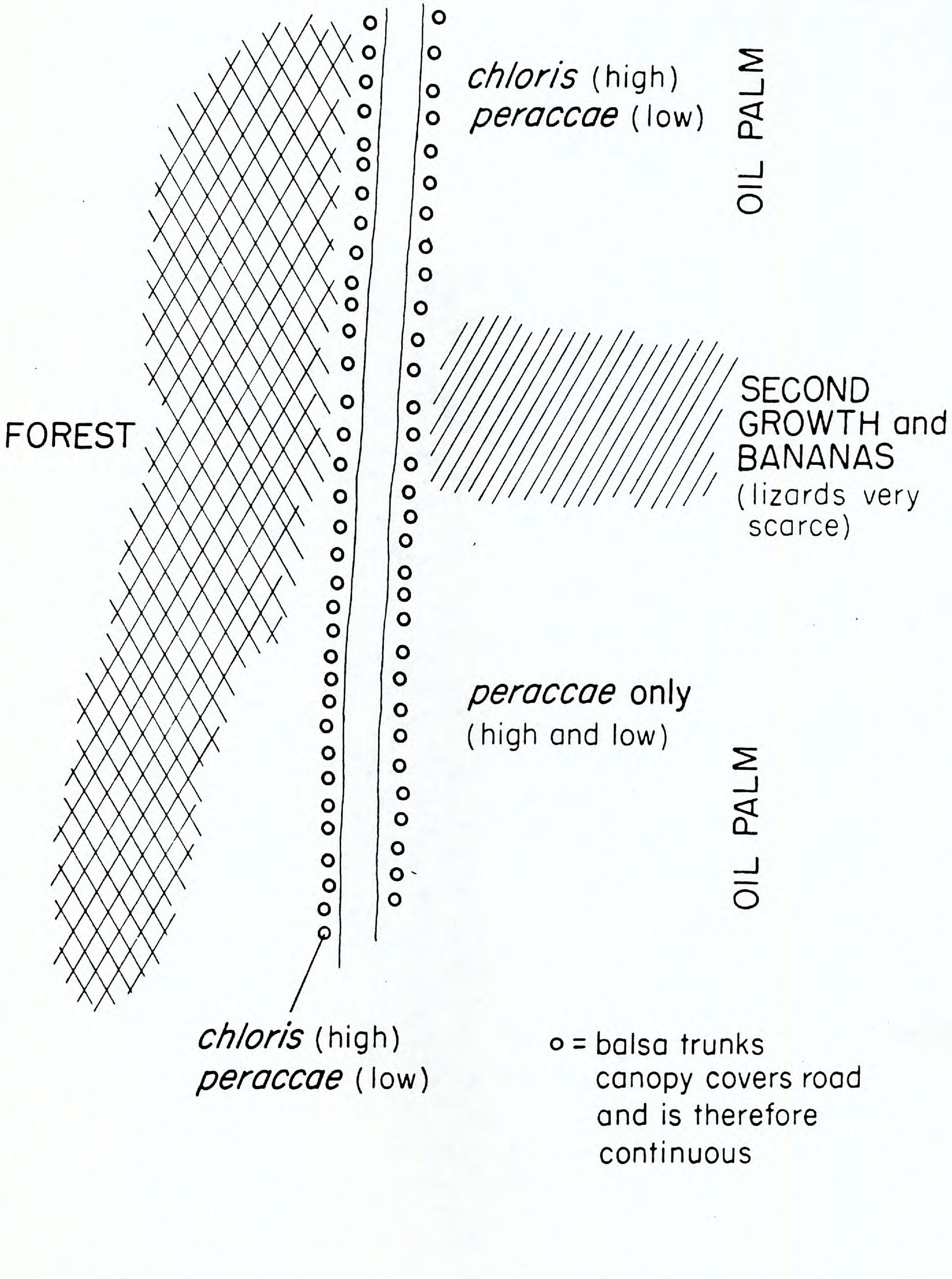


FIG. 1
Perch height (inches)

FIG. 2


1974
n = 292
1975
n = 539
1976
n = 123
FREQUENCY
HEIGHT (inches)
0 20 40 60 80 100 120 140 160 180 200 220 >220


OIL PALM
chloris (high)
peraccae (low)
SECOND GROWTH and BANANAS
(lizards very scarce)
FOREST
peraccae only
(high and low)
OIL PALM
chloris (high)
peraccae (low)
o = balsa trunks
canopy covers road
and is therefore
continuous

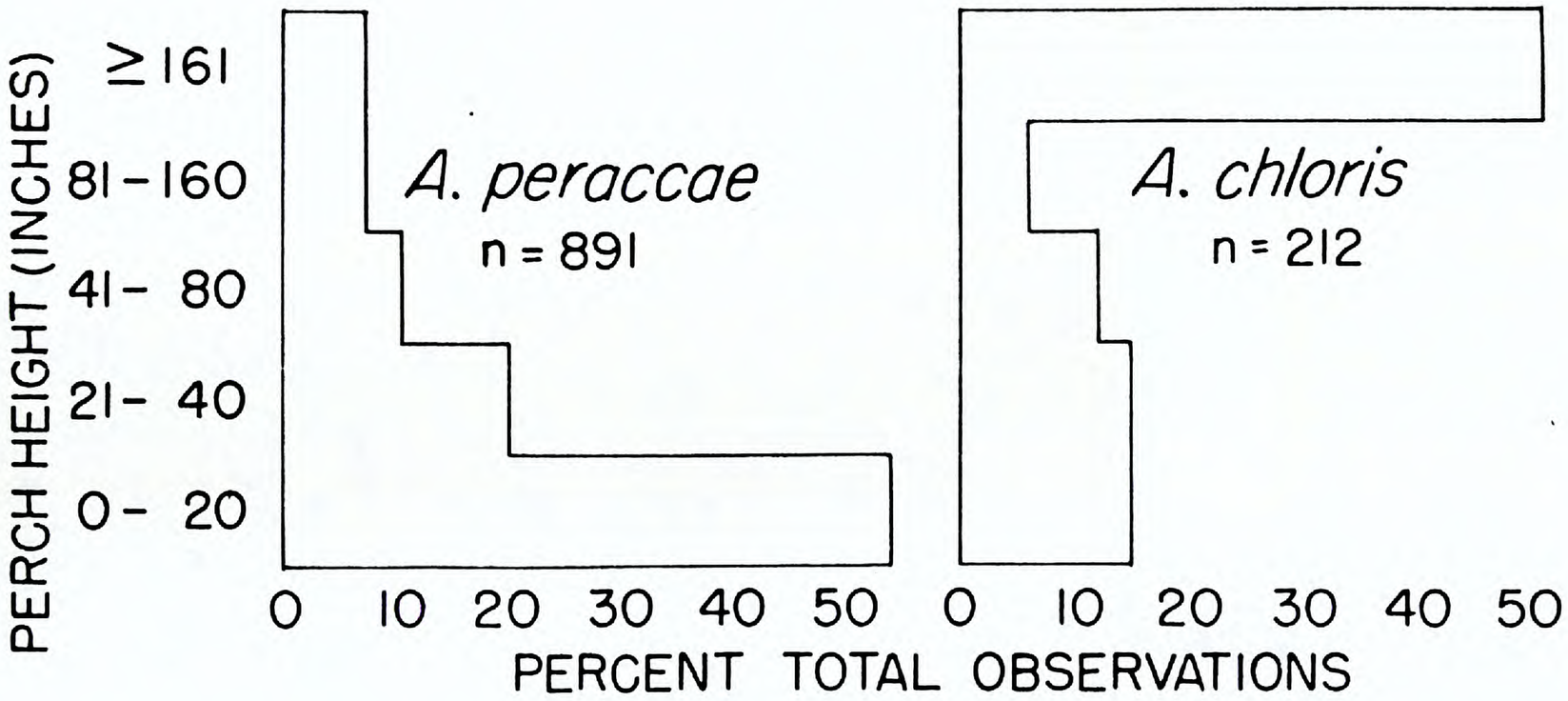
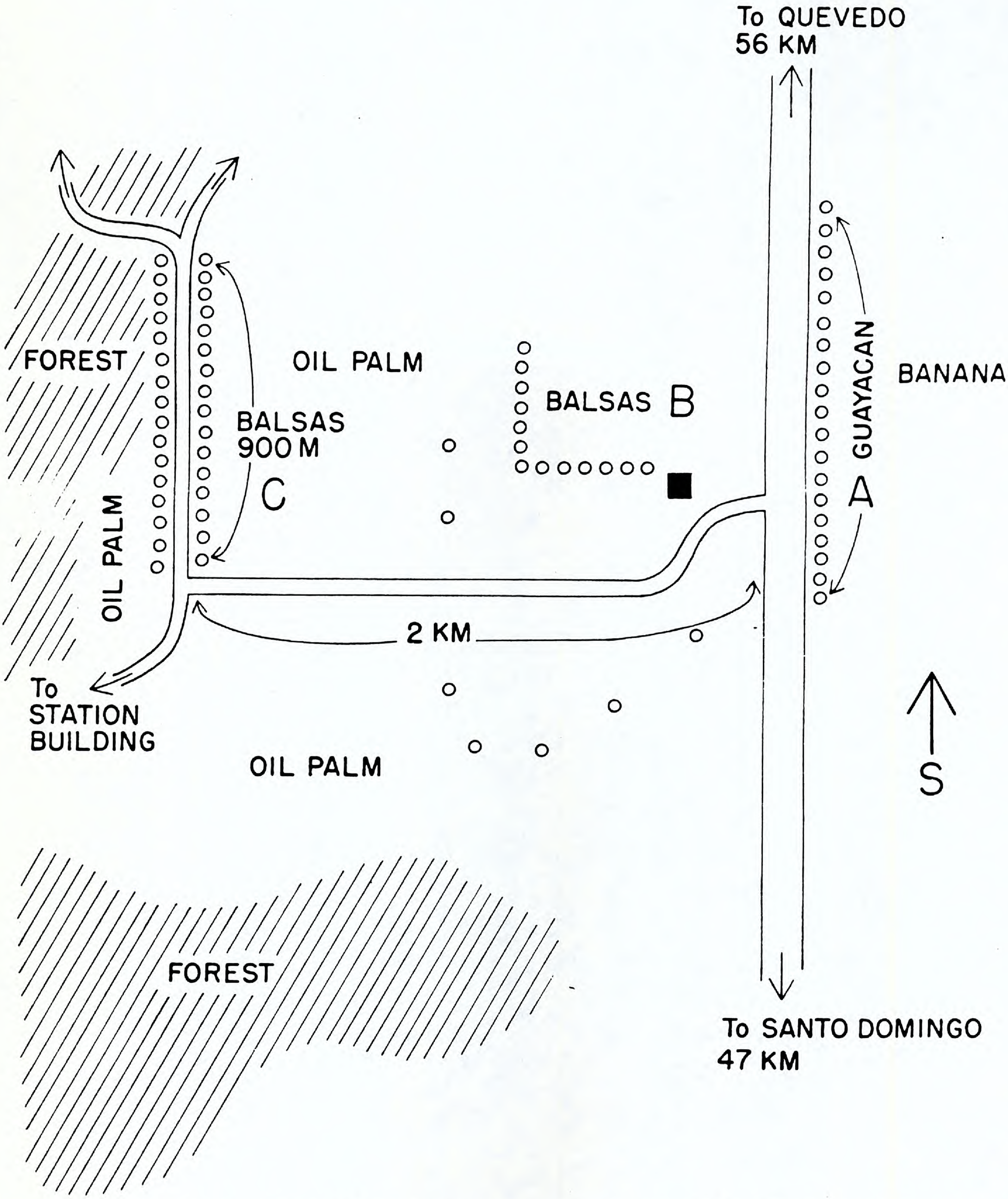

PERCH HEIGHT (INCHES)
≥ 161
81 - 160
41 - 80
21 - 40
0 - 20
A. peraccae
n = 891
A. chloris
n = 212
0 10 20 30 40 50
0 10 20 30 40 50
PERCENT TOTAL OBSERVATIONS

FIG. 4



Sketch map of cultivated tree rows at Rio Palenque

TIMOTHY MOERMOND (Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706) continues his work in the Lesser Antilles and has begun work also in Puerto Rico.

He has now seen the following Lesser Antillean species in the field:

Species	Island	Minutes of recorded observations
A. aeneus	Grenada	~ 2500
A. richardi	Grenada	~ 3000
A. griseus	St. Vincent	~ 800
A. luciae	St. Lucia	284.9
A. extremus	St. Lucia	74.7
A. roquet	Martinique (lowlands)	~ 2000
A. roquet	Martinique (highlands)	~ 1500
A. oculatus	Dominica	~ 1200
A. marmoratus	Guadeloupe	~ 400
A. bimaculatus	St. Kitts	~ 2500
A. wattsi	St. Kitts	~ 2000
A. wattsi	Antigua	~ 600
A. leachi	Antigua	~ 800

His comments on these species follow:

One of the continuing points of interest in Anolis ecology is the parallel patterns of habitat partitioning among the communities of the Greater Antilles. I have proposed a conceptual model for the influence of habitat perch structure on the movement patterns and morphology of Anolis and hence on the pattern of habitat partitioning. It was tempting to test its application on one- and two-species communities such as those found in the Lesser Antilles. Not only are there two divergent stocks (the bimaculatus group and the roquet group) with replicates of each community type, but the preliminary size patterns analyzed by Schoener (Amer. Nat. 104: 164) showed striking similarities with most two-species communities comprised of one large and one small member and most solitary forms being intermediate.

Earlier observations have suggested that the species pairs are also separated by climatic preferences - one being found primarily in sunny open habitats, the other in shade (Schoener and Gorman, Ecology 49: 819-830).

In my recent studies I have used three types of data: morphological measures from preserved specimens, timed observations of foraging behavior and movement in the field, and measures of the perch matrix being occupied by a given set of lizards. This last measure uses a modification of the quarter-point method of vegetation analysis. Essentially the dispersion and characters of perches about a lizard are measured by using the perch of a freshly sighted lizard as the center of a horizontal plane, and including the nearest adjacent perch in each of four quadrants radiating in that plane. The distances to these other perches are recorded as well as the lengths and diameters of all five perches. Only the diameters will be used below as in each case the diameter distribution is a reliable index of the relation of all three measures. The patterns of habitat use for the two-species islands of Grenada and St. Kitts as I now view them are summarized below.

Richardi and aeneus; Grenada.

Over the island aeneus is apparently the only common species in the driest habitats while richardi is decidedly the most common in the cool dark forest around the Grand Etang, at 560 meters. Nevertheless, overlap is considerable over a wide range of elevations and habitats.

Observations of movement patterns were taken for both species at a lowland scrub and a montane forest site and limited observations were taken on richardi in the forest at the Grand Etang. Measurements of the perch matrix were taken for both species at the lowland scrub site but only for richardi in the montane forest. At the latter site richardi was abundant in the semi-natural forest but aeneus was primarily present only in adjacent open plots of planted Hibiscus trees.

Bimaculatus and wattsi; St. Kitts.

Earlier observations of this pair suggest that the smaller species, wattsi, is the one limited to shade while bimaculatus is characteristically the sun species. My experiences suggest that bimaculatus is most abundant in well-developed second growth of mango and breadfruit, although it was also found commonly on roadside trees, dooryards, and coconut groves. The largest males were found only in the heavy second growth at medium elevations (Bayford Estate) where they were common. Bimaculatus was not found in the rain forest.

In contrast, wattsi was found commonly in all habitats sampled, from the dense, dark rain forest to the driest, most open thorn scrub at Frigate Bay, where bimaculatus was decidedly less abundant (a crude estimate of relative density with wattsi may be 1 to 10). Although the wattsi in open habitats appeared to be more active near dusk, they were observed actively foraging in early afternoon in both the Frigate Bay scrub and Conaree Beach coconut palm debris.

In a sample of similar dry scrub on Antigua (Falmouth), leachi (the equivalent of bimaculatus) was decidedly more numerous, although wattsi was still numerically dominant.

Behavior observations were made for both species in the dry scrub at Falmouth, Antigua and at six sites in St. Kitts with additional observations of wattsi at two rain forest sites. Measurements of the perch matrix were taken in rain forest, second growth, and dry scrub for wattsi and in only the latter two for bimaculatus, although its scarcity in the dry scrub precluded obtaining enough points for a reliable sample.

Perch matrices.

A comparison of the perch diameter distributions for wattsi in three habitat types appears in Figure 1. Note the strong similarities. A further comparison of wattsi in the dry scrub site on St. Kitts with that for Antigua (Figure 2) shows a similar resenblance. A comparison of the perch diameters associated with each species in the second growth, however, shows striking differences (Figure 3). Clearly within the same habitat, the two species are occupying decidedly different perch matrices.

If a similar comparison is made for wattsi and leachi in the dry scrub site on Antigua (Figure 4), the difference is less dramatic but consistent with leachi occupying a matrix with larger diameter perches. The smaller magnitude of the difference is likely due to the lack of larger diameter perches in the scrub - only one or two trees on the site had trunks greater than twelve inches in diameter.

In contrast to the perch matrix differences noted above, a similar comparison for aeneus and richardi (solid lines in Figure 5) shows only minor differences suggesting essentially no separation in the perch matrix occupied by these two species in the dry scrub sampled. The added sample of richardi at a forest site shows only slight but expected deviations.

Morphological comparison.

Observations on aeneus and richardi reported in the Second Anolis Newsletter revealed striking differences in the movement patterns of these two species which are reflected in correlated differences in limb to body proportions (Figure 6). Thus, although these two species occupy essentially the same perch matrix, they use the perches in a different manner. It should be noted that the juveniles which overlap in body size also differ in microhabitat (see the Second ANL). This was not reflected in the perch matrix measure of Figure 5 as very few young were present at the time those measures were taken.

In contrast, behavioral differences in the movement patterns of wattsi and bimaculatus are not readily apparent at this early stage in analysis and, consistent with this, their limb proportions show little difference (Figure 7), both species somewhat resembling richardi.

The implications with regard to the differences in the matter of habitat partitioning of the two species pairs are important. The pattern of partitioning in richardi and aeneus may be largely due to differing foraging styles with attendant changes in morphology, while in bimaculatus and wattsi partitioning may be due to a division of the habitat according to the perch matrix. The differences in size in this latter pair may primarily reflect adjustment to the 'size' of the perch matrix occupied. If this is the case, then one would expect the juvenile bimaculatus to overlap the denser matrix of wattsi and therefore they may possibly be in competition with wattsi. The restriction of bimaculatus in habitat range may be related to this competition. This remains to be studied further.

Single species islands.

I now have sample observations on foraging and behavior for the solitary species of Guadeloupe, Dominica, Martinique, and St. Lucia, with the most complete data for Martinique. At this point, morphological analysis has been done only for two populations of roquet, but perch matrix data has been collected for lowland scrub and montane forest habitats for both roquet and oculatus.

Superficially all age classes of roquet observed in the northwest lowlands of Martinique resembled those of A. aeneus in their movement patterns. Particularly the large adult male roquet were quite active. The rate of prey capture of roquet appeared to be higher than that for aeneus on Grenada but this may be a consequence of the fact that the observations on aeneus were made in December and those on roquet in July. The deep shade areas in lowland scrub that in Grenada are occupied by juvenile richardi close to the ground appear to be vacant in Martinique.

Preliminary comparisons of the behavior and limb proportions for two populations of roquet (lowland scrub and montane forest) show deviations which appear to be correlated with differences in the perch matrices occupied at the two sites. Analysis now in progress on like pairs of populations on Dominica suggests a similar pattern. Although the field portion of this particular comparison will be unable to be extended to other islands within the next couple of years, morphological analysis of analogous populations is planned for Guadeloupe and St. Lucia.

Future plans.

1) Morphological comparisons of limb proportions will be extended to most of the Lesser Antillean species, to various populations within a species where possible, and to certain species on Puerto Rico and Hispaniola. A fair body of data has already been taken for several Haitian species but this needs to be expanded.

2) Artificial perch matrices have been constructed in observation chambers at Wisconsin and are presently occupied by leachi and wattsi. Preliminary observations of movement patterns of leachi in these chambers has provided information on the importance of perch separation with regard to jumping abilities. This type of observation is very difficult to make in field situations.

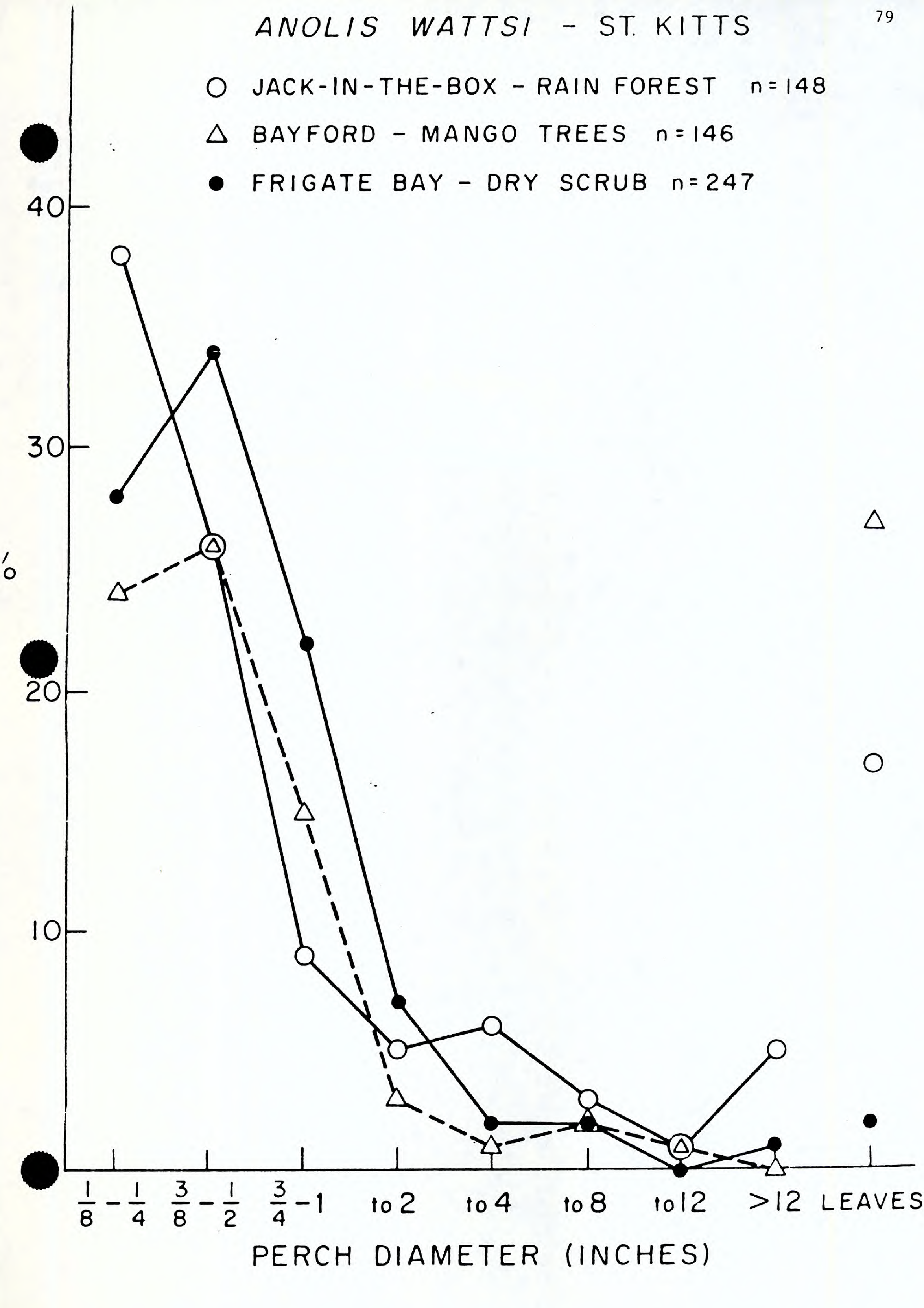
3) In the summer of 1977 I plan expanded field studies of the behavior and the perch matrices of bimaculatus and its related forms and wattsi on a range of habitats in St. Kitts, Antigua, and St. Martin. In addition, I plan to apply the perch matrix measures to the Haitian species for which I already have considerable behavioral data.

ANOLIS WATTSI - ST. KITTS

○ JACK-IN-THE-BOX - RAIN FOREST n=148

△ BAYFORD - MANGO TREES n=146

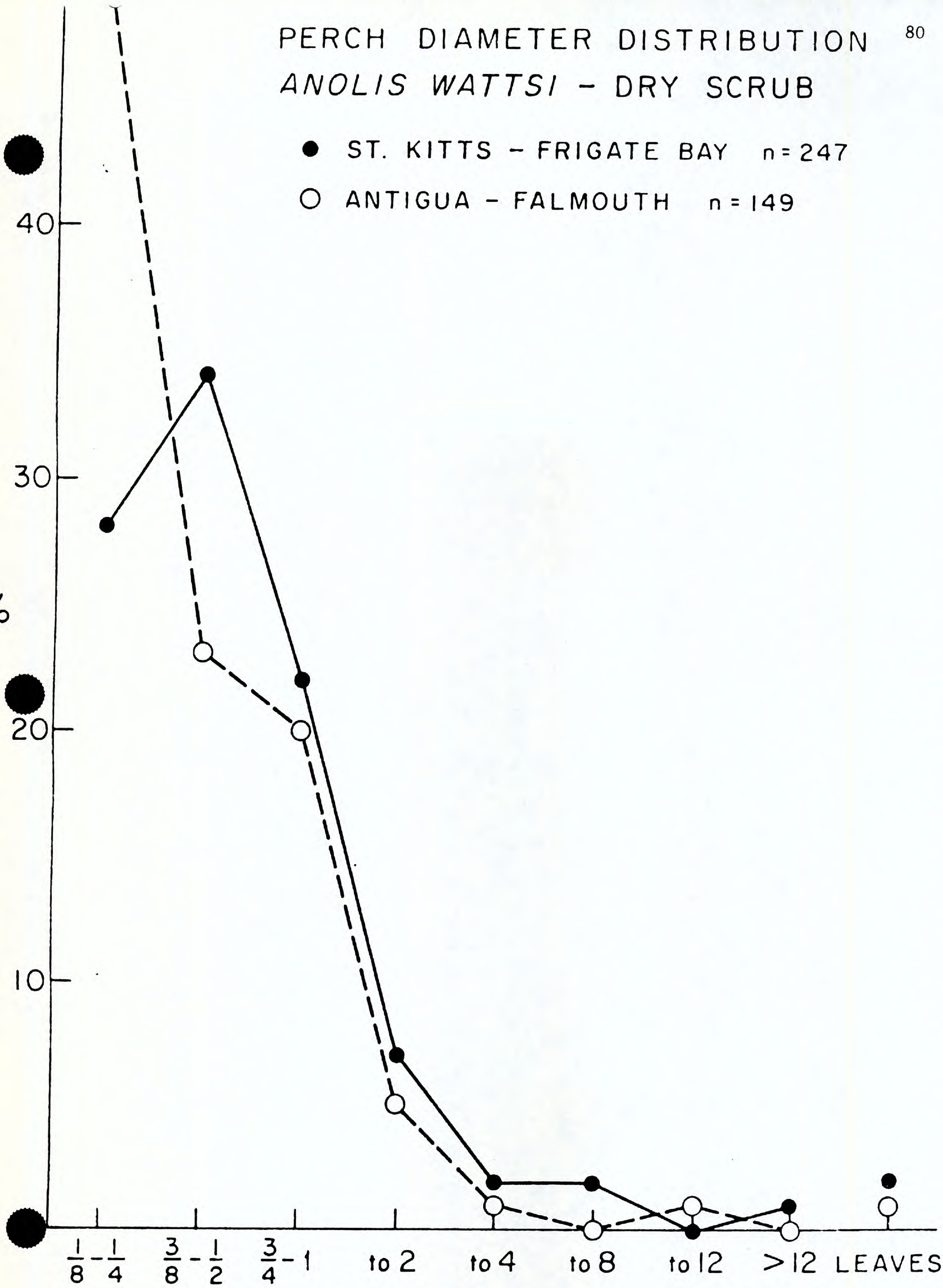
● FRIGATE BAY - DRY SCRUB n=247



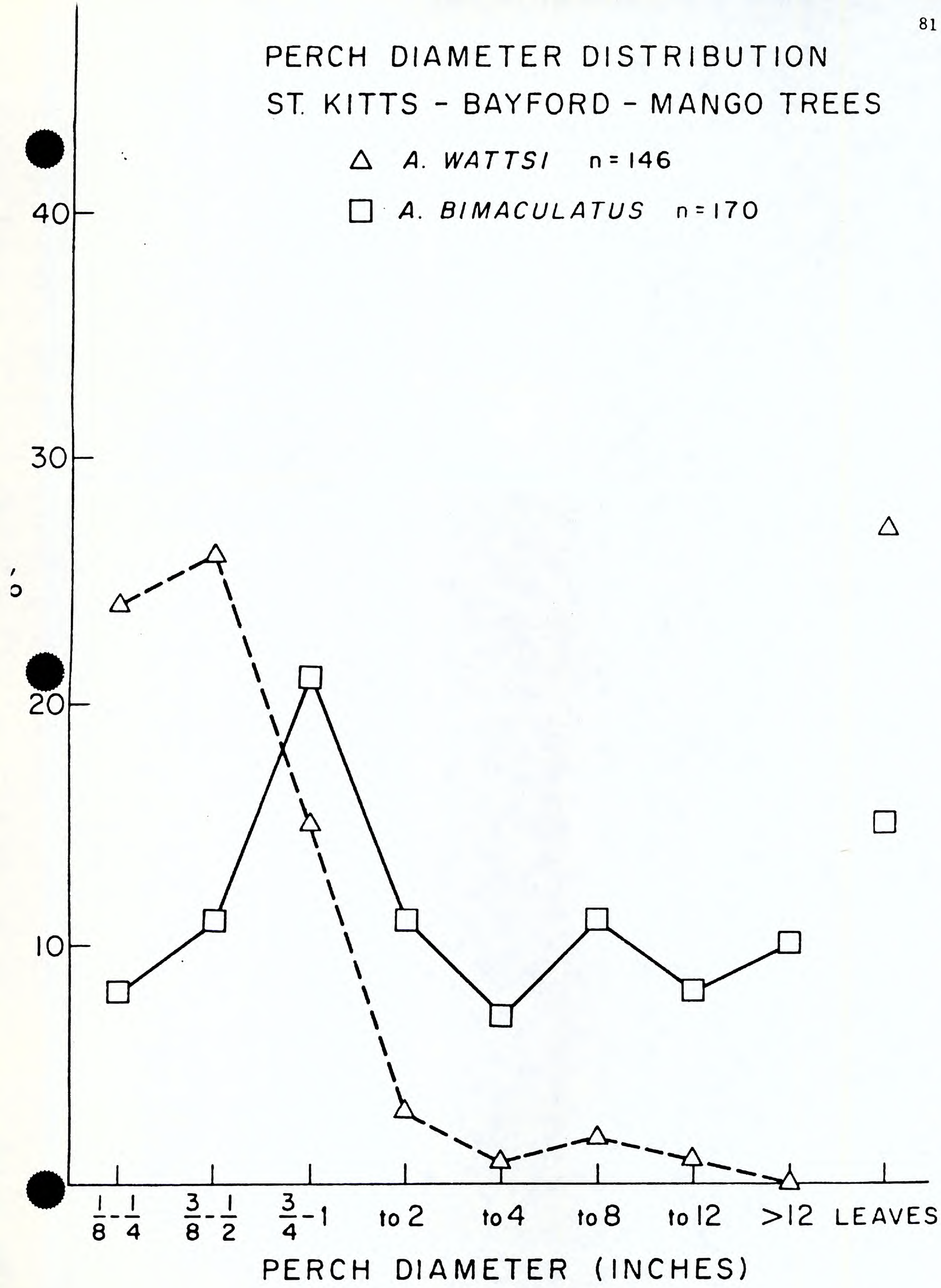
PERCH DIAMETER DISTRIBUTION
ANOLIS WATTSI – DRY SCRUB

● ST. KITTS – FRIGATE BAY n = 247

○ ANTIGUA – FALMOUTH n = 149



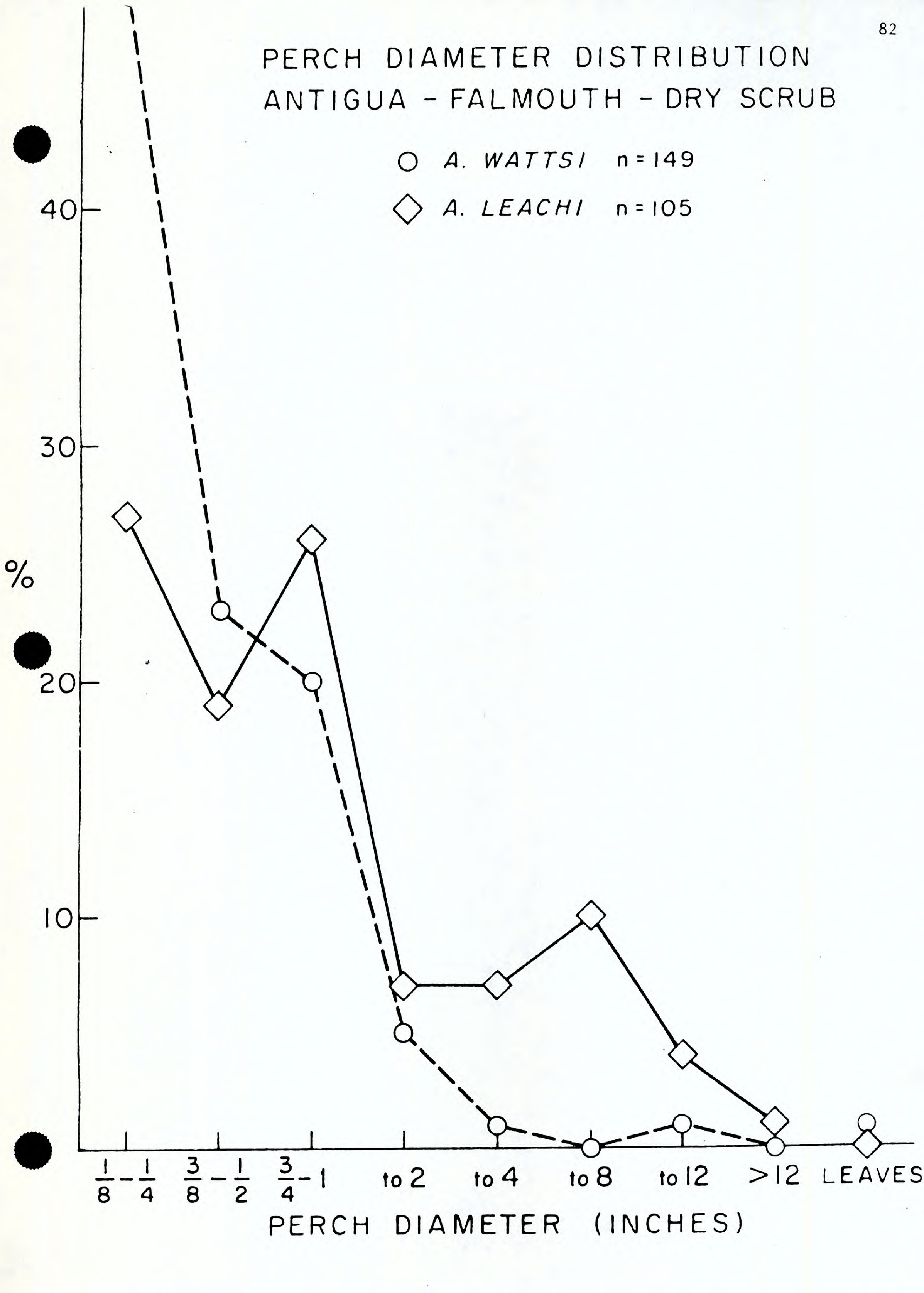
PERCH DIAMETER DISTRIBUTION
ST. KITTS - BAYFORD - MANGO TREES



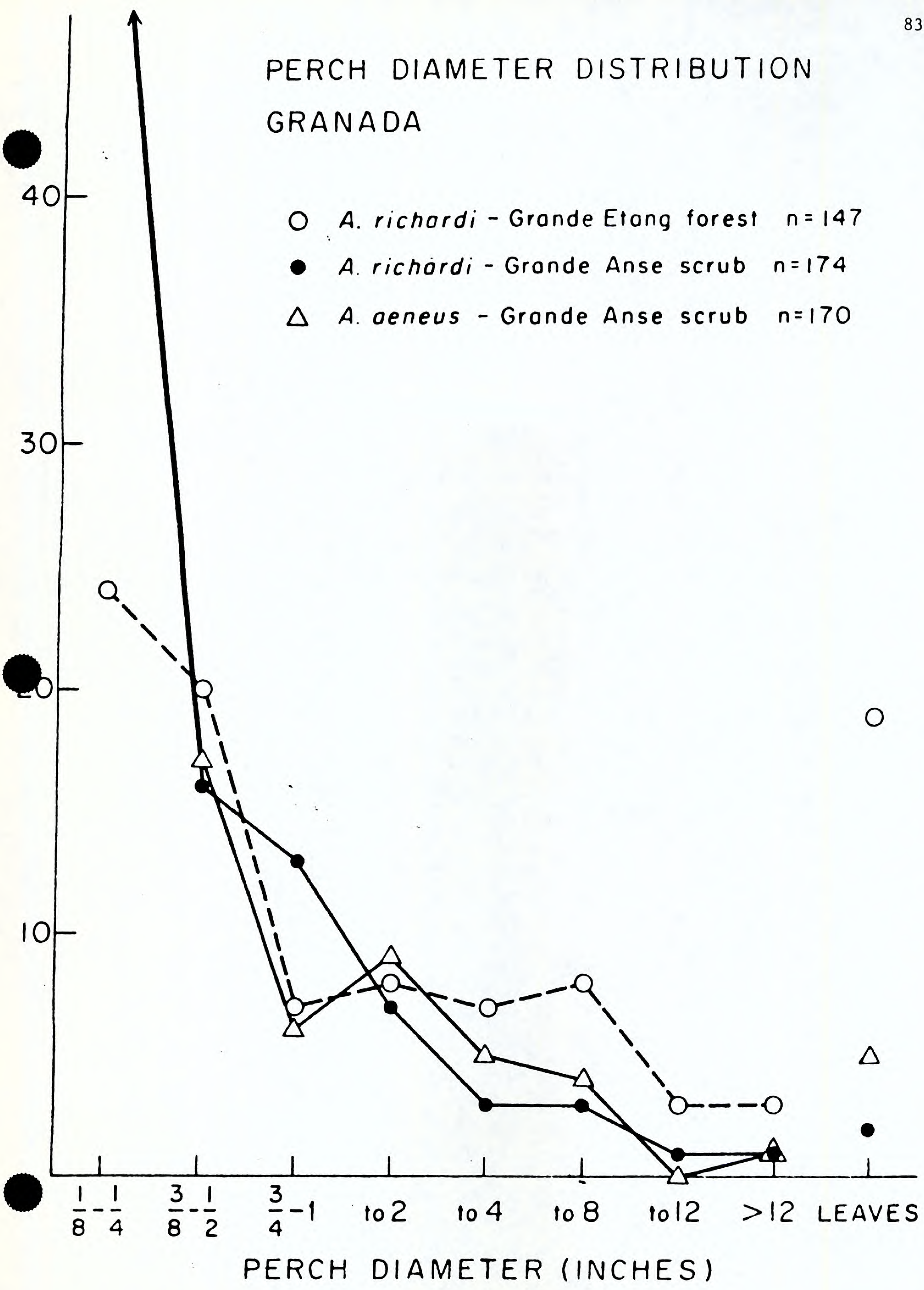
PERCH DIAMETER DISTRIBUTION
ANTIGUA - FALMOUTH - DRY SCRUB

○ *A. WATTSI* n = 149

◇ *A. LEACHI* n = 105



PERCH DIAMETER DISTRIBUTION
GRANADA



SNOUT-VENT V.S. FEMUR + TIBIA

o *Anolis aeneus*, n = 39

x *Anolis richardi*, n = 134

FEMUR + TIBIA

SNOUT-VENT

SNOUT-VENT V.S. FEMUR + TIBIA

o *Anolis wattsi*, n = 33

x *A. bimaculatus*, n = 38

FEMUR + TIBIA

70
60
50
40
30
20
10
0

10 20 30 40 50 60 70 80 90 100

SNOUT-VENT

A. S. RAND (Smithsonian Tropical Research Institute, Balboa, Canal Zone) reports a new device for the study of lizard behavior: The animated anole, or "Lizard Theater for Lizards."

Building on techniques pioneered by Tom Jenssen, Anne Parker, with Stanley Rand's direction and help from Olga Wallace, has developed an animated anole display film.

Anolis auratus was selected to work with because a great deal is known about its displays, it is available locally in Panama, and it lives well in captivity and reacts easily and reliably in test cages.

The first activity was to film a large number of A. auratus signature displays in the laboratory at 54 frames a second. From these films traditional DAP graphs of the signature display were prepared from frame-by-frame analysis of head and dewlap positions (Figure 1a). Working from a number of signature DAPs, a generalized or "typical" signature DAP was drawn and then modified so that it could be represented at 18 frames per second (Figure 1b).

A series of tracings of a displaying lizard were made showing its shape and position at each stage of the display. From these drawings the major movement units in the lizard's image were identified and the pivot points between them located.

A two-dimensional model lizard was constructed from thin clear acetate sheets or cels. Each of the major movement units was drawn on a different cel and these were jointed at the appropriate pivot points (Figure 2). Each of the cels had an extension marked with a pointer to indicate its position. The "back" cel pointer read on a scale fixed to the background and indicated its position relative to this. Each of the other cels had a pointer which read on a scale fixed to the cel on which it pivoted so that its position was indicated relative to the rest of the lizard rather than to the background (Figure 3).

Using the display films and the tracings made from them, the jointed model was maneuvered through the positions assumed by a displaying lizard. The movements of the various pieces of the model were analyzed in a series of graphs (Figure 4). From the graphs and the pointer readings corresponding to them, a script was written (Figure 5) which specified the positions that the various components of the jointed model should take at each of the various steps in a display.

The model was painted as naturalistically as possible and a dewlap designed.

The dewlap in A. auratus is black with rows of bright yellow scales. The model was to be filmed against a black background, so the dewlap was designed as a series of rows of yellow dots, each on a separate clear cel and each pivoting independently (Figure 6). The dots represented the scales and the black background showing through between them represented the black skin of the dewlap.

With the model complete and the shooting script ready, the animation was filmed using KII film in a Nizo S-80 Super-8 camera. The model was moved into the position specified by the shooting script, a single frame was exposed, the model was moved to the next position, the next frame exposed, and so on. Even using 18 frames per second, instead of 54, filming was a long process.

While Anne Parker had been working on the films, Stanley Rand had been developing a test apparatus to use them. They knew from Tom Jenssen's earlier work that Anolis would respond to movies and also that he had had difficulties with eliciting responses from A. limifrons. Rather than use Tom's female choice as an assay of the effectiveness of their displays, they decided on the much more easily elicited male display.

They already knew that two male A. auratus placed in a bare cage would usually begin to display at one another and a quite prolonged and intensive encounter might ensue. In its willingness to display in a strange place, A. auratus contrasted with some other anoles from which it was difficult to elicit displays except in the case of males who were within what they recognized as their own territories.

The next step, taken before they invested much in film, was to determine that A. auratus males would display to their own image in a mirror. This they did by taping a small rear-projection screen against the glass side of a cage and positioning the projector so that the image of the lizard was about natural size. They found that films taken (and shown) at 54 fps and 18 fps both elicited displays.

To satisfy themselves, and carping bystanders who suggested that A. auratus males would display at anything, they made a brief excursion into puppets. Remembering Jenssen's criticisms of other work, they did not mechanize the operation but merely presented to the male A. auratus, just on the other side of the glass of his cage, an A. auratus male, freshly fixed in formalin, in a natural position, and moved up and down by a thin monofilament thread. They could elicit no responses to these models whether with dewlap folded or open. These negative results led them to drop puppeteering and persist in cinematography.

A lizard theater was then built to allow the lizard being tested a choice of perches, but ensuring that from all of them he could see the screen. The theater was largely made of screen and wood and whatever glass was used was slanted to eliminate the complications introduced by the lizard seeing and displaying to his own reflection.

The projector was positioned behind the projection screen and the cage lighted from above so that the screen received minimal illumination. The room was darkened during tests and the observer located so that he could see, and if desired film, both lizard and movie screen. The test films consisted of about 1/2 minute without motion. The initial trials of the animated display have evoked responses from the adult A. auratus males that consist of

the typical signature display. This is qualitatively the response which they give to a live displaying male. (Nothing is yet known about the quantitative differences, if any, in the responses.)

The animation technique seems a very promising tool (as well as being a fun thing in and of itself). Parker and Rand's first use of it has been to attack the problem of redundancy in display situations. Rand and Williams, 1970, argued, on the basis of the differences between sympatric anoles in Hispaniola, that species differ routinely by more than a single characteristic. They further argued that "species identity" was coded redundantly in this way and they postulated that a lizard had available, and could use, several alternative ways of identifying a conspecific.

Parker and Rand have started to test this with A. auratus by designing two animation models, one with the species specific color and pattern and the other a simple generalized anole silhouette. Each of the models was filmed doing two displays: 1) the species typical (and specific) signature bob and flash and 2) a series of regular bobs and flashes of about the same length of time as the signature display but differing from it in that the bob and flashes are all the same rather than having the typical pattern.

The next step is to attempt to dissect the display further and ask what level of redundancy exists between the components of the display (e.g., bob vs. dewlap flash). Also to be tested is the reaction of A. auratus to similar sympatric species (A. limifrons and A. tropidogaster) to see if there is some sort of special "inhibition" against reaction to their appearance or display.

Beyond the redundancy question, the next aspect of display that Parker and Rand can investigate is that of size. Relative size is believed to be very important in social interactions in anoles, but direct evidence is scant. By moving the projector closer to or further away from the test screen, they can vary the size of the stimulus they are presenting without affecting any other parameters. Once they have determined the effect of overall size they can vary independently different aspects of size such as the area of the dewlap, the depth of the body, and the snout-vent length. They (Williams and Rand, in prep.) are suggesting elsewhere that a number of display elements serve to increase the apparent size of a displaying animal. By the animation techniques they can test this idea directly by measuring responses to models.

Another idea which could be tested with the animation technique relates to the complexity of signature displays. It is clear that these displays are complex in their patterning even in species which do not occur with any other. The sole exception seems to be A. agassizi. Having watched and filmed anole displays in the field, Rand is impressed by the amount of movement that occurs in a natural environment, because of air currents moving leaves and sticks, etc. This is most evident in the open areas where the foliage is almost always moving but also occurs deep inside the forest, though there are fewer things moving there and they tend to move less violently.

The forest is seldom completely still for long. This movement of the environment is perhaps an important and largely ignored element in the evolution of lizard displays. This "background" movement provides a screen behind which an anole can conceal his display movements from visual predators. Leaves in the breeze tend to move up and down or back and forth in an oscillatory manner. Animals, such as Chameleons, Polychrus, Mantids, Vine Snakes, Phasmids, etc., which move slowly through the foliage frequently adopt an oscillatory movement, a rocking or teetering which mimics the movement of wind-activated leaves and so conceals the animal's own movements.

In the same way, by using a basically oscillatory movement for its display, a displaying anole reduces the likelihood of its being noticed by a predator. However, as much as the displaying animal wants to avoid the attention of a predator, it must attract the attention of the conspecific to whom the display is directed. Rand suggests that the complex, stereotype movements of the signature display are what make it recognizable by the conspecific amongst the variety of other movements with which it occurs in the environment. A species of Anolis can presumably evolve a mechanism for the easy and/or rapid recognition and identification of a single movement pattern. A predator faced with a wide variety of movements which it is important that he recognize would be less likely to be able to cue on the pattern of an anole display.

If a major function of the pattern of a signature display is to distinguish the lizard's movements from the movements of surrounding leaves, etc., one understands why solitary species retain complex displays and why A. agassizi, living on an island with virtually no vegetation, has evolved a simple display. This view of display leaves dewlap color completely unexplained.

Rand hopes to be able to develop this idea and by analyzing the kinds of movements that leaves, etc. exhibit in the natural environments make some predictions about the movement patterns that A. auratus should recognize and those which it should ignore. He then hopes to generate some animated films that will test the predictions.

This by no means exhausts the ways in which the animation technique could be used but it does exhaust the time currently available to spend on this project.

FIGURE CAPTIONS

Figure 1. Display action pattern graphs for the A. auratus signature display. Major modifications in animating display:

1. Display starts and finishes at same level.
2. Length of bobs adjusted to necessities of 18 fps filming.
3. Step added in last bob and antipenultimate bob shortened because sample display differed from usual display in these two regards.

Figure 2. Model showing individual cels and their joints.

Figure 3. Model showing the fixed scale and one of the several relative scales.

Figure 4. Three stages in the analysis of the movements in a two-step bob. In step A→B: lifting of back (⅓ 1), bending back of neck (⅓ 2), lowering of nose (⅓ 3) which diminishes absolute change. In step B→C, most of change is due to neck pulling back.

Figure 5. Filming script indicating the positions for the various cels during each step in a two-step bob lasting 1/8 second.

Figure 6. Dewlap model showing individual cels.

Figure 7. Test apparatus for showing animated films to real A. auratus and for recording responses.

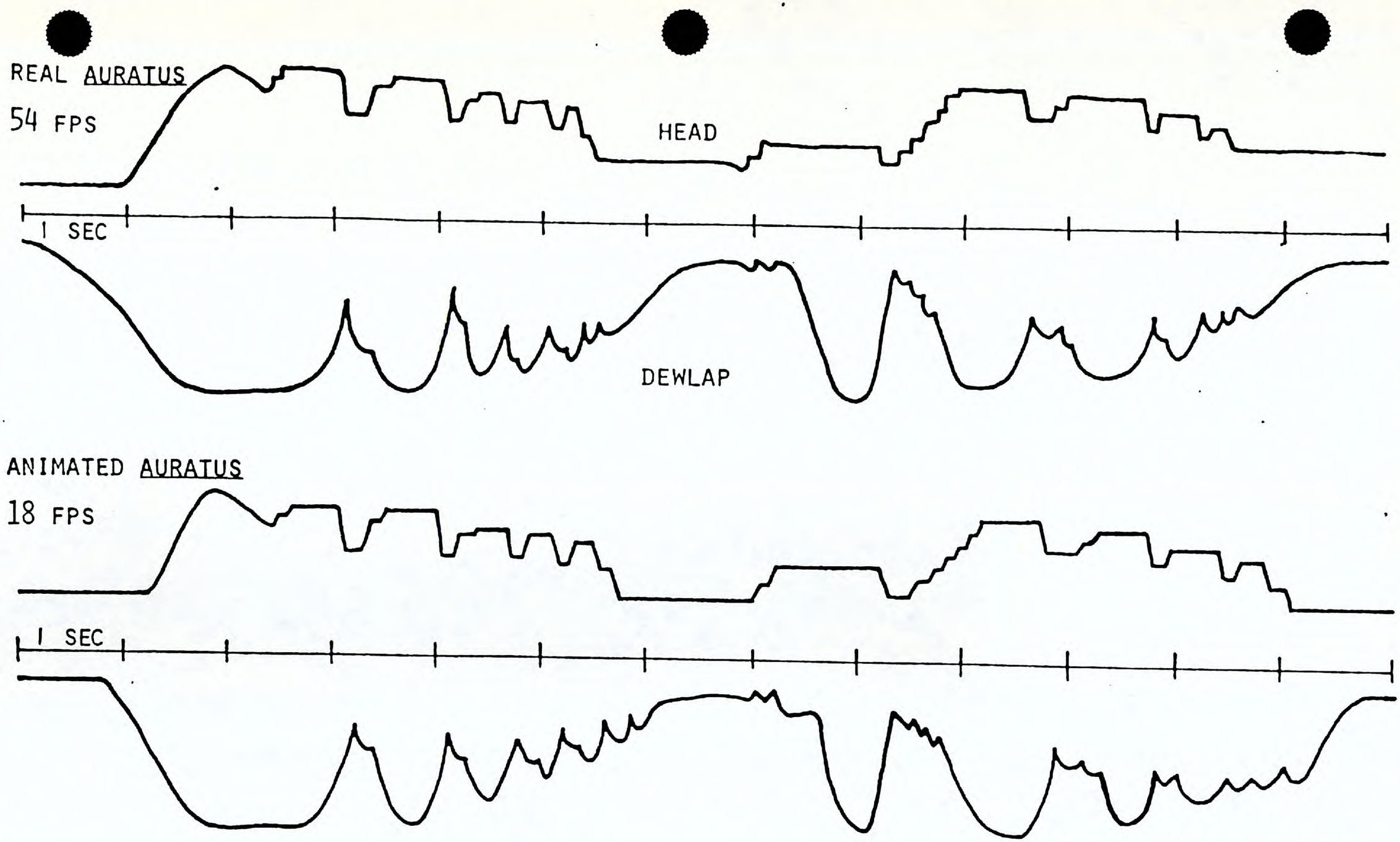

REAL AURATUS
54 FPS
HEAD
1 SEC
DEWLAP
ANIMATED AURATUS
18 FPS
1 SEC

FIG. 1

FIG. 2

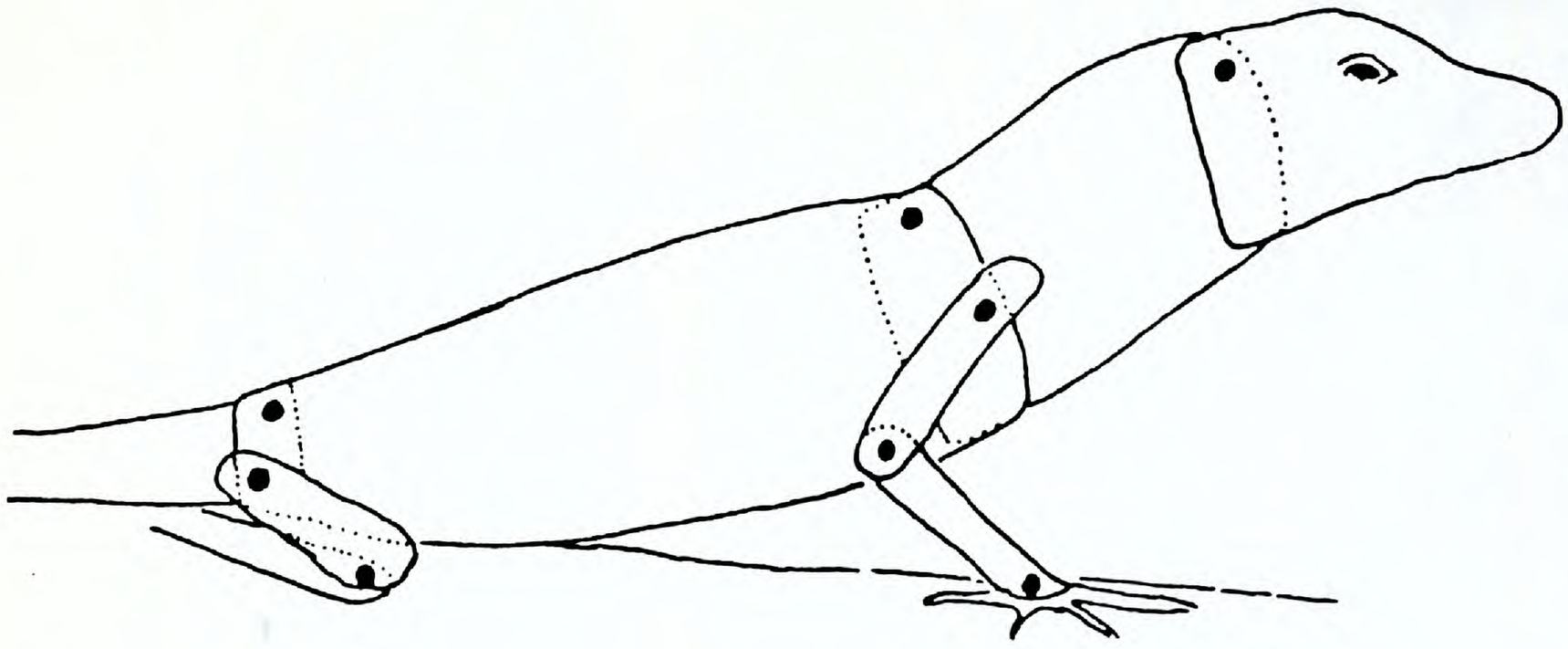


FIG. 3

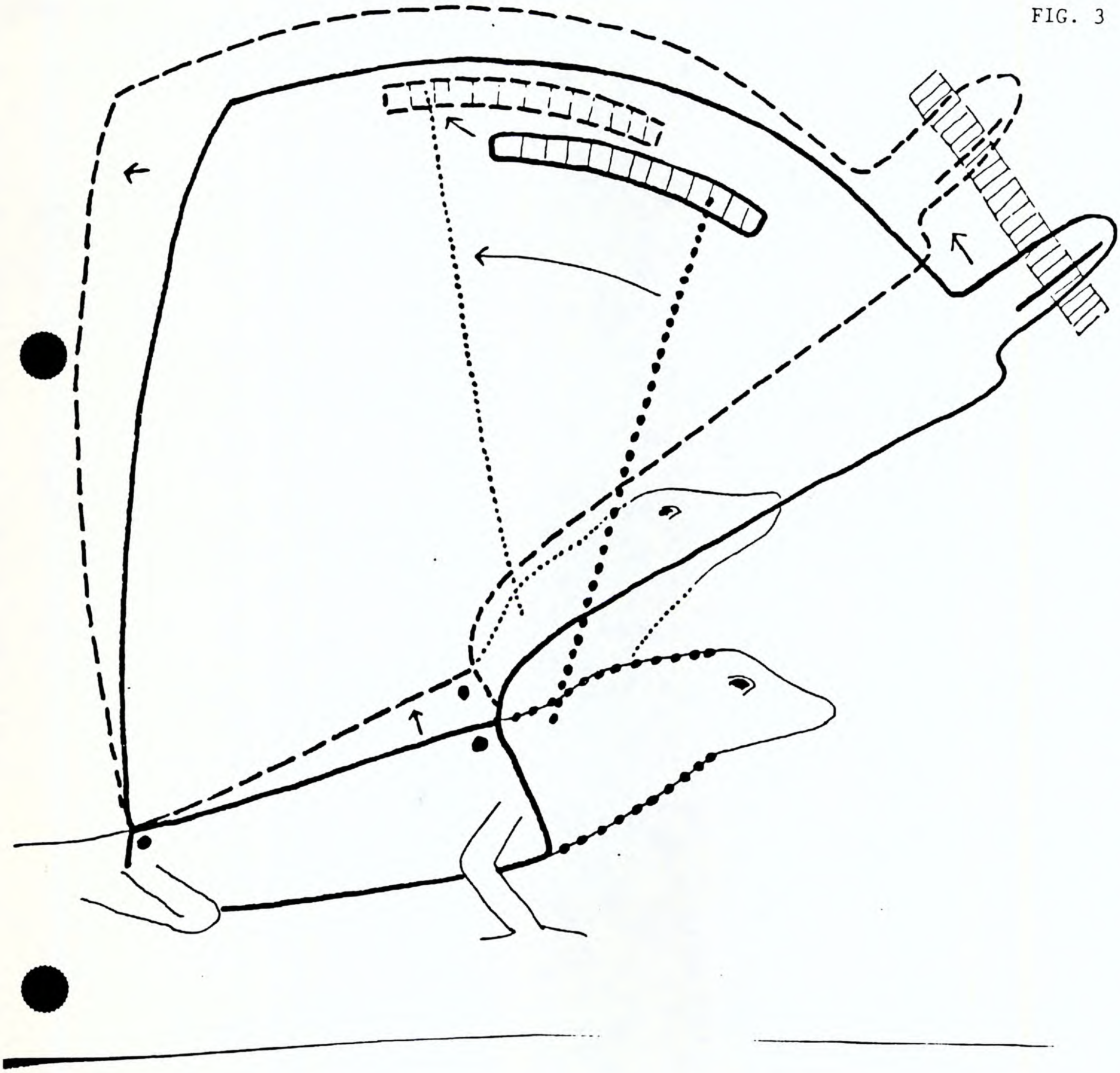


FIG. 4

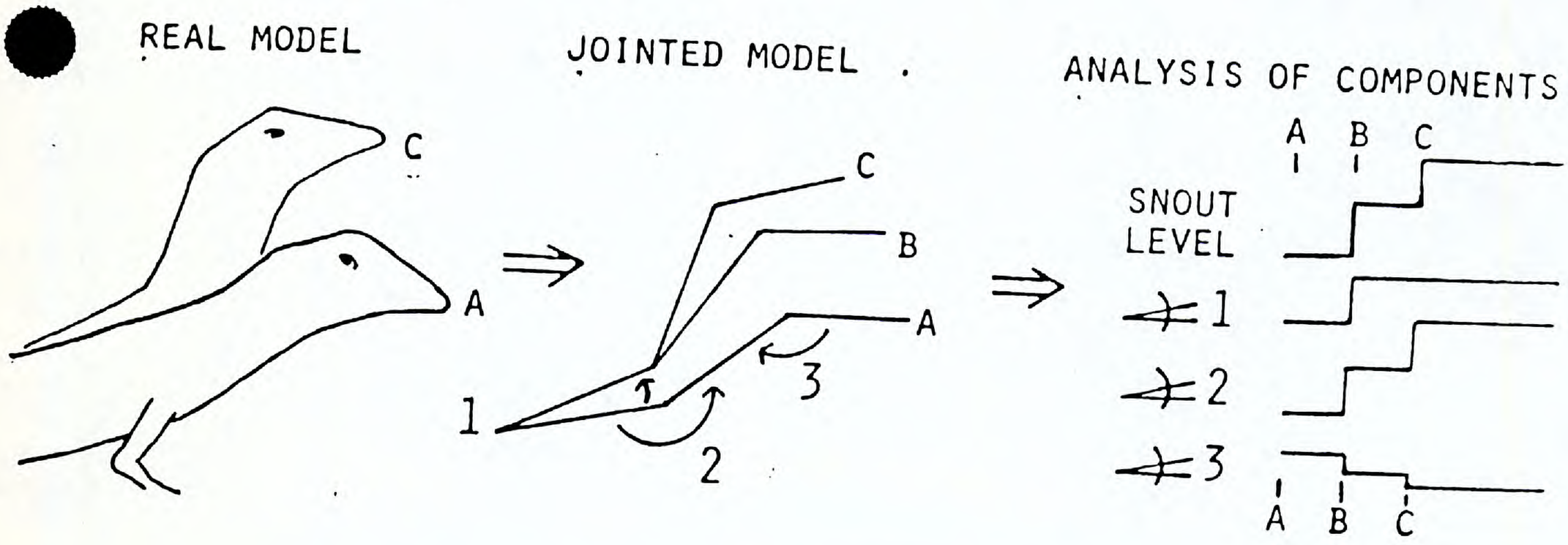


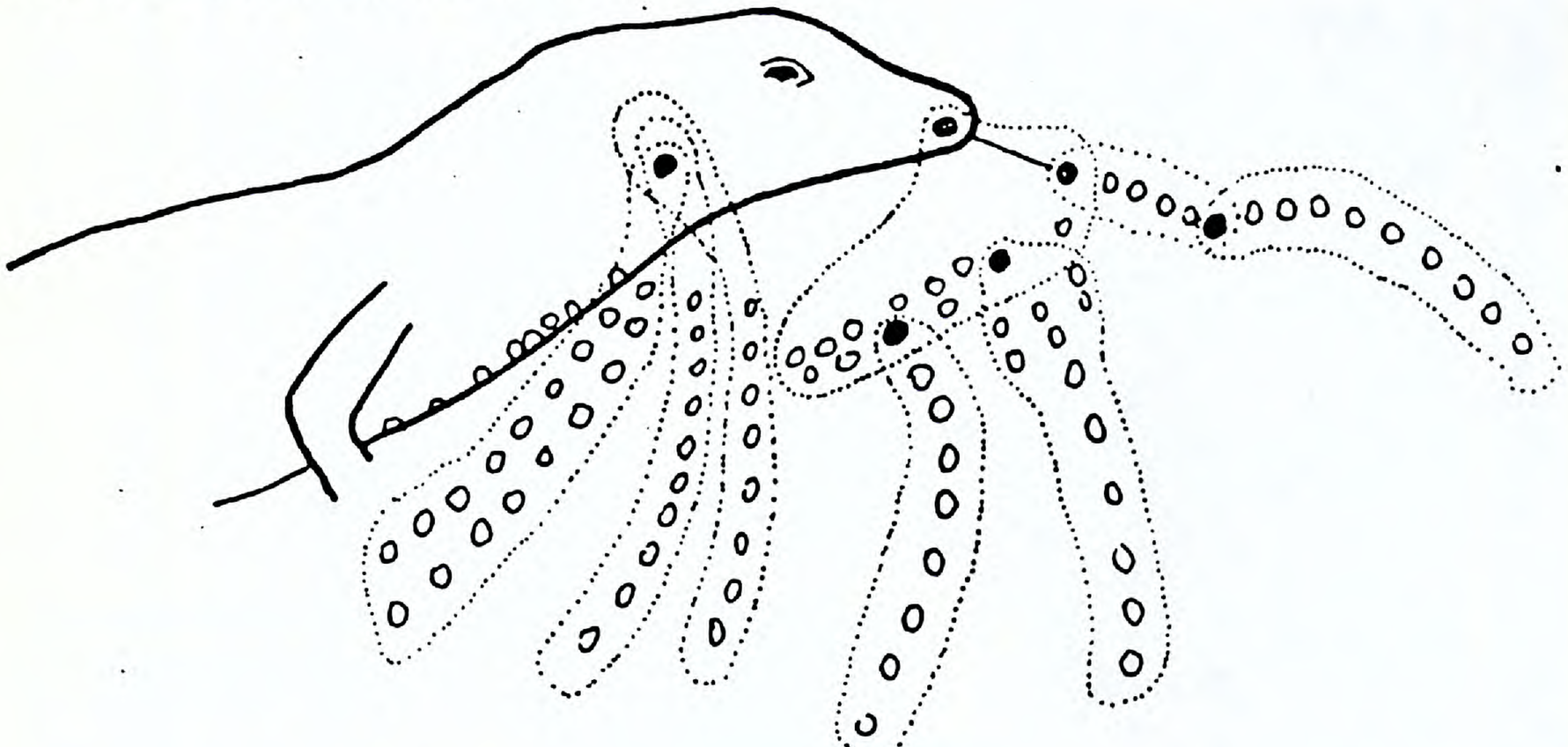
FIG. 5

MOVIE SCRIPT : TWO STEP BOB

FRAME	LEVEL	BACK	NECK	HEAD	DEWLAP
48	HOLD	13½	15½	15	20½
49	"	"	"	"	23
50	"	"	"	"	25½
51	UP	14	19	12	24
52	HOLD	"	"	"	"
53	"	"	"	"	25
54	UP	"	22½	11	26
55	HOLD	"	"		27

FIG. 6

DEWLAP MODEL WITH PARTS EXTENDED



DEWLAP MODEL IN TWO POSITIONS

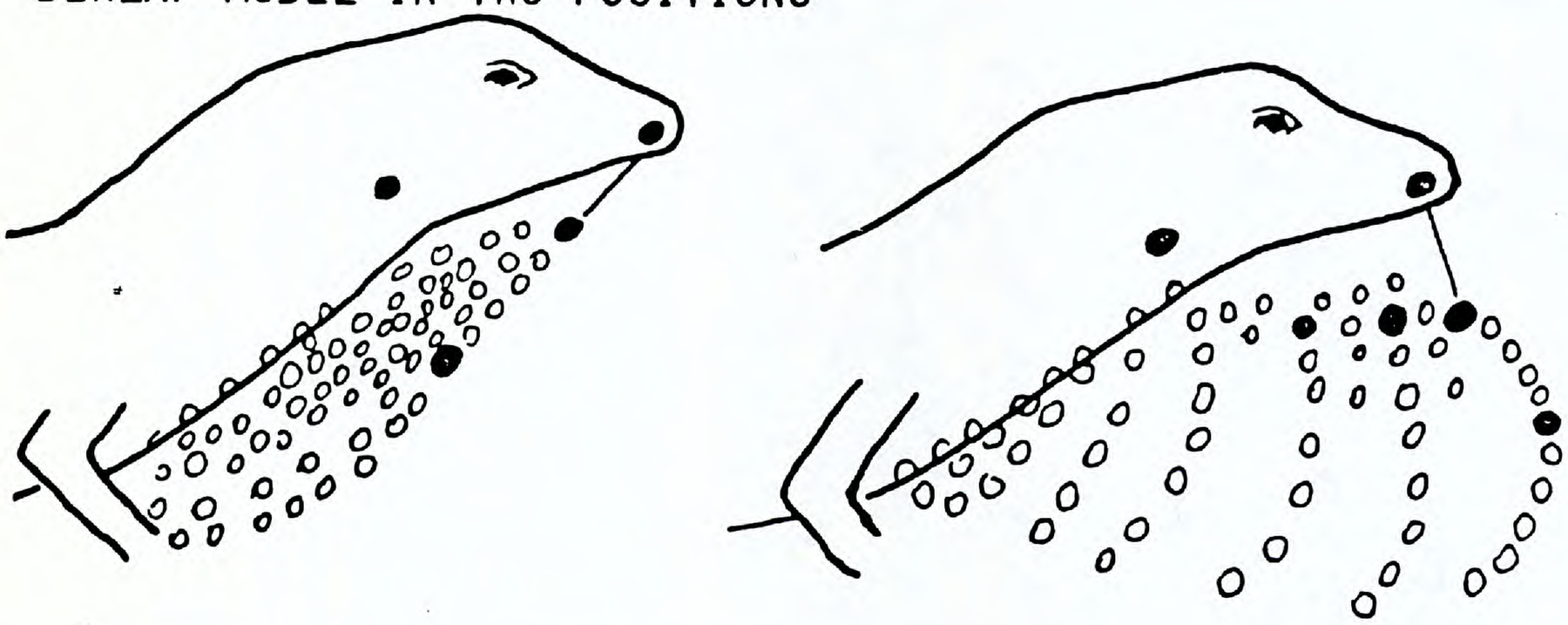
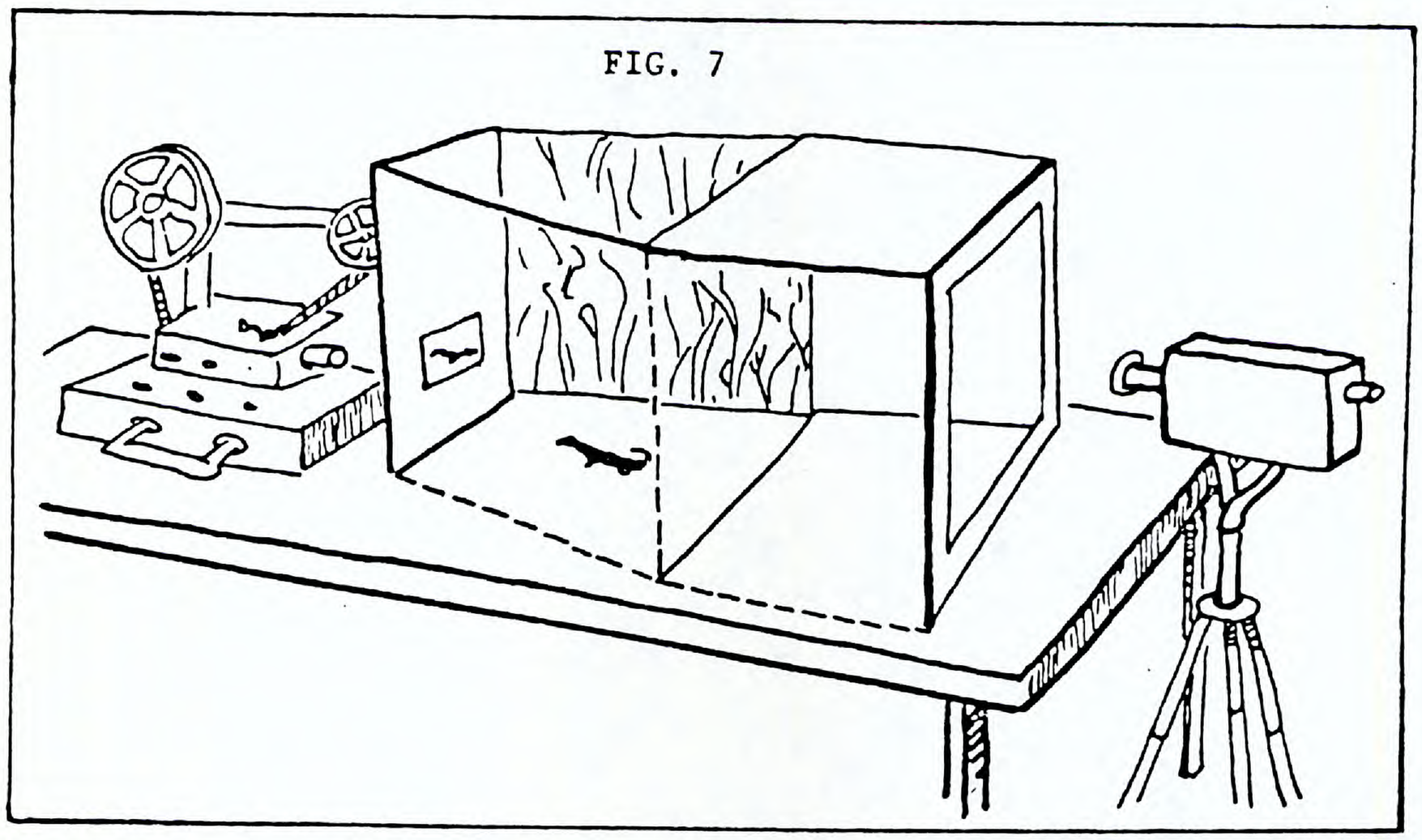


FIG. 7



With Stella Guerrero, Rand has been studying lizard malaria. They report as follows:

Over the past several months we have been studying malaria in free-living anoles in the forest on Barro Colorado Island in the Panama Canal Zone.

Since early rainy season in 1976 we have been sampling the anoles in two small study areas at bimonthly intervals. Lizards are caught, measured, weighed, marked, a blood sample taken and then released within 24 hours at the spot where they were originally captured. Blood slides are stained and examined for parasites.

The data collected on these anoles are being analyzed as part of a demographic study of this population (see Robin Andrews), in addition to our attempts to assess the effects of their malaria.

Three species of malaria are present: Plasmodium balli, P. tropiduri, and P. floridense. All three are known only from reptiles but are not specific to Anolis limifrons. The species differ in their apparent effects on the RBC's that they infect, P. balli appearing to be a much more damaging parasite than are the other two. All may occur in the same animal.

A preliminary analysis of the data for the rainy season in the Lutz Watershed site has been reported at the IV International Symposium on Tropical Biology, March 1977, Panama. Malaria has been present throughout the rainy season and new cases appear between each pair of censuses. The level of infection in adults is high; between 50 and 70% adults are infected at each census.

Comparing infected with uninfected adults on the basis of our preliminary analysis, we are unable to detect an effect of chronic malaria on: length-weight relationships; survival; growth rate; or frequency of oogenesis. The data do suggest that adults that are infected with malaria have a much higher probability of surviving the initial phases of the disease and bringing it under control than do the juveniles.

During the next several months we propose (1) to continue our field studies of the incidence and effects of malaria on free-living Anolis limifrons, (2) to support a study attempting to identify the vector of the disease and (3) to initiate laboratory studies of the course of the disease in captive lizards.

Several other parasites have been observed in Anolis limifrons. The most important of these is a liver nematode. This has been tentatively identified as belonging to the genus Capillaria. This parasite seems to have a much more serious effect on its host than do the Plasmodium species under study. Several anoles have died in captivity soon after capture and have been found, on autopsy, to have the liver tissue almost completely replaced by these nematodes and their eggs. No nematode eggs have been found in either the feces or blood of even heavily infected anoles and we suspect that this nematode, like others in the genus, usually kills its host. We are collecting information about the incidence of this parasite and its life cycle.

RICHARD SALVATO (Department of Surgery, J. Hillis Miller Health Center, University of Florida, Gainesville 32611) has studied the activity of Anolis garmani in dry forest (broken canopy and sparse understory) near Kingston, Jamaica.

Data was collected during a three-week period, August to September 1974, supplemented by two weeks in November 1974.

A group of 10 males and 10 females, marked by toe clipping and paint, were watched for fifteen 30-minute periods (a total of 450 minutes). Additional observations were made on the lizards at times other than the 30-minute periods of concentrated observation. The time spent in various activities and the perch height at which these activities occurred were recorded. Body temperatures were also recorded.

Results: Social interactions for males occur at higher perches than those determined for overall male activity. Although males must move down to feed, either to locate prey or because more prey is found at lower levels, they still feed at significantly higher levels than females. Immatures use perches only slightly lower than females.

Females spend 62% of their time in feeding activities, while males spend only 20%. Males spend 56% of their time in social activity - 43% in male-male interaction and 13% in dewlapping. Every male holding a territory was seen to spend some portion of each day, typically after descending from the upper portion of the vegetation, dewlapping, usually toward no discernible target.

23% of male activity and 30% of female activity had to be recorded as unclassified. In males such periods were motionless pauses, often in the sun. Thermoregulation may be involved or watching for conspecifics or for predators.

Males and females occupy lower perches during the late morning and early afternoon than during the early morning or late afternoon. During the hours of lower perches, more lizards were found in the sun than in the shade. Body temperature was also higher.

THOMAS W. SCHOENER AND AMY SCHOENER (Departments of Zoology and Oceanography, University of Washington, Seattle 98195) are continuing their Bahaman researches. After a year's rest from one lengthy and spectacular boat trip, they are back from a similar trip, a little less adventurous but hardly less ambitious.

1. The first boat trip.

The results of the first trip in Spring 1974 were sufficiently interesting to encourage the Schoeners to propose and the National Science Foundation to provide some additional funds for the 1976 operation. The following is a report of the first voyage:

In a small boat with an owner crew of two, Schoener and Schoener censused birds and lizards on 15 selected archipelagos along a 500 mile line transect from the Crooked-Acklins bank northward through the Great Bahamas, visiting all islands down to and somewhat below sizes which lacked diurnal vertebrates.

On each island maximal vegetational diversity was measured, i.e., the area was located at which vegetation was tallest. A grid was put down such that the enclosed area could have supported 100 individuals of the commonest anole on a main island. Within selected quadrants all diameters at critical heights in the vegetation were determined and the angles of inclination were measured. With the aid of this information, relative surface area of perches at the several height intervals (and other measures of vegetational availability) can be calculated.

From detailed maps drawn from aerial photographs, the area of each island was determined, as well as the area of each type of macrohabitat (mangrove, sandy scrub etc.), the distance to nearest island, to nearest larger island, to nearest main island, maximum elevation, and other variables.

Taken together, this data permitted ordering of the islands in terms of the variables cited or of variables computed from those cited (i.e., measures of foliage diversity, contour diversity, horizontal habitat diversity).

In analysis each variable thus far has been treated separately (multivariate approaches will be done later) with the objective of discovering which variable best predicts presence or absence of certain species, and also if certain species are better predicted by any variable than are others.

Results: 1. Birds and some lizards are predicted by foliage availability as well as or better than by area.

Thus an understory lizard such as A. sagrei is best predicted by amount of foliage greater than one foot. Anolis carolinensis, a crown lizard, is best predicted by higher foliage. Foliage insectivorous birds are best predicted by amount of foliage greater than 3 ft. Foliage herbivorous birds are best predicted by amount of foliage greater than 3 ft, 5 ft. or 7 ft. Ground herbivorous birds are best predicted by amount of foliage greater than 3 ft., but ground or arboreal lizards better by area of island.

2. In general, area is a better predictor for lizards, foliage availability for birds.

3. Measures of foliage height diversity are good predictors also, especially for ground lizards. Perhaps the result for ground lizards is due to the need for behavioral thermoregulation. (Lizards also have the sexes and ages of quite different size and habitat preference.)

4. Area affords very regular prediction for lizards but less so for birds. This is true both for individual species and for all species combined. In fact, for the Crooked-Acklins bank, if area is plotted against species number, only one island is out of place (by one island). The relationship in birds is much less monotonic.

5. Distance is seldom a good predictor by itself - except for herons and birds that don't breed on islands but fly to them to feed, and except for migrants where the relation is inverse. But distance, unlike foliage measures, foliage diversity, altitude measures and horizontal habitat diversity, is truly independent of area and hence should be more important in multivariate analysis.

6. Lizards are sensitive to small changes in distance. Birds are not. Thus a lizard-species area plot is significantly lower for islands 10 miles from a source area than for groups less than one mile from the source. Birds show absolutely no difference over this range.

7. Bird species are able to exist on islands in much smaller population sizes than lizards. Thus, the same island that might have 100 Leiocephalus might have a pair of bananaquits or mockingbirds. (Birds compensate for their higher extinction rate in any given area by the higher immigration rate, i.e., their much greater dispersal ability.)

8. Lizards seem to equilibrate their relative abundances over great distances on land but not over even very small over-water distances. For example, on the 10-mile long Fortune Island of the southern Bahamas, Anolis carolinensis is the most abundant diurnal lizard at one end as well as the other. Yet on a small fringing island less than 100 yards away from the north end, where carolinensis does not occur, Anolis sagrei and Leiocephalus become far more important, and the latter especially seems to expand its variety of horizontal habitats.

9. Lizards occur typically on islands down to areas of 10^4 ft^{+2}. Thus, perhaps 10^4 or 10^5 islands in the Bahamas have lizards.

10. There is great regularity in the presence or absence of most lizard species. In some archipelagos species increased with area in a nearly monotonic way, and faunal lists were often perfectly nested. This means that precise thresholds exist below which a species does not occur and above which it does. Since the islands are more or less randomly arranged with respect to area, it is sometimes possible to find islands of nearly but not quite equal area with different faunas. The possibility for a highly controlled and natural set of removal-introduction experiments is great, and the Schoeners

have just received funding to do such experiments.

11. One taxon, Leiocephalus, has an apparently capricious distribution. It occurs on clumps of islands large and small and does not occur on other clumps of islands large and small. No obvious physical or biological barriers separate the two sets of islands.

A possible historical explanation is the following: Leiocephalus has a very generalized diet and a preference for open habitats. It may, on the one hand, have been forced into marginal low diversity habitats on the main big islands, and it may, on the other, prefer open habitats for thermal reasons. In either case, it would be more restricted in its habitats than the other species when the present-day Bahaman islands were united into larger islands by the low sea levels of the Pleistocene. Then when sea level rose, certain newly created islands had few Leiocephalus and others had many. The more the islands fragmented, the more Leiocephalus thrived on the ones it happened to be abundant on; on others, it never occurred or went extinct. Schoener has now formulated a competition model that accounts for the stability of this pattern and which will be tested by introductions and removals.

12. In terms of area, Leiocephalus is the first species in the sequence, occurring on the smallest islands. A. sagrei is the second species in the sequence, but occurs on islands with and without Leiocephalus - on smaller islands if Leiocephalus is absent than when the latter is present.

2. Survival and persistence survey.

At the end of their long trip the Schoeners visited Andros and Bimini as part of their long term studies of marked Bahaman populations.

Results: (1) 99% of lizards marked in 1970 are now dead on Bimini. But some have survived at least four years, perhaps five.

(2) On Andros male sagrei in optimal habitats are nearly all gone and females about 2/3 gone. On Bimini there has been much better survival for males, and somewhat better for females. Sex differences in survival for angusticeps are much less different for the two islands.

Interpretation: Sagrei on Andros is under much greater mortality pressure, possibly from predation by or competition with Andros' more diverse bird fauna (lizard diversity on the two islands is identical). Notice that this affects males, which behave more conspicuously, more than females.

Greater bird diversity may explain sagrei's smaller size on Andros than on Bimini. (Perhaps Andros sagrei males mature at a smaller size than Bimini males, and they do not have the time to grow as large as on Bimini.)

Angusticeps males and females would not be under as much differential pressure from predation since both are cryptic. Angusticeps does have a lower recapture rate on Andros than on Bimini, presumably again because of greater predation or competition, but again sex differences are not obvious.

3. The second boat trip.

The 1976 boat trip surveyed two further Bahaman banks (San Salvador and Little Bahama) and involved a lizard fauna significantly different (e.g., fewer anole species) from that of the 1974 trip. The results complement those obtained in the first boat trip and suggest introduction-removal experiments additional to those previously planned.

On the islands surrounding San Salvador, the Schoeners found Anolis distichus, the third or fourth species in the lizard sequence on the Great Bahama bank, to be the first species here. Leiocephalus was represented by a species different from the other banks, one which is smaller and more restricted in habitat. This was the second species in the sequence. A. sagrei, the only other species on the bank, was almost restricted to the main island. This order of species additions is precisely the opposite of sequences found before and suggests 1) that sagrei is a recent arrival to the San Salvador area, colonizing after the small islands became separated (testable by introduction of small sagrei propagules), and 2) that Leiocephalus is the first species in the sequence on the Great Bahama bank and Crooked bank by virtue of its large size; where it is smaller it loses much of its competitive advantage. This is supported by observations that very large Leiocephalus eat Anolis.

The islands of the Little Bahama bank have a base diurnal lizard fauna of only two species, Anolis sagrei and Leiocephalus carinatus, perhaps because of their northerly and peripheral location. The lowered lizard diversity is here often complemented by a high avian diversity, higher on the average than islands farther south. Here, sagrei is almost always the first species in the sequence, and in some places Leiocephalus is restricted to the largest islands. One has the impression that Leiocephalus carinatus is here a marginal species, perhaps because of unfavorable thermoregulatory conditions. The competitive advantage seems to have shifted to sagrei. Experiments will test this hypothesis.

Comparison of bird and lizard patterns on these northern islands extends and confirms the trends discovered farther south. Five or six species of birds, those capable of breeding on the small islands, can be found as solitary species. More complicated avian communities are relatively variable. Lizard communities, as reported, are more constant.

JUDY STAMPS (Department of Zoology, University of California, Davis, California 95616) continues to study the social and spacing behavior of Anolis aeneus.

Work recently completed includes the following:

1. The survey posture (head pointed down, extended out from the body) in Anolis aeneus functions mainly in the detection of food. Percent of time spent in the survey posture was compared before and after feeding to satiation on termites. Before experimental feeding lizards spent most of their time in survey position; after feeding the time spent in this position dropped precipitously.

2. A comparative study of juvenile lizards indicates that juveniles of either sex give all of the displays characteristic of adults except for the courtship bob. Juvenile displays are as stereotyped within individuals as are those of adults. Interindividual variation in the species specific signature bob is the same in juveniles and adults. Interindividual variation in two other bob patterns (jerkbob, multibob) is greater in juveniles than in adults, perhaps an example of stabilizing selection. Juveniles are more apt to give certain aggressive displays spontaneously than are adults.

3. Juveniles are more agressive than are adults of either sex to very large or very small intruders into the home range. When intruders are very small, adults tend to ignore them while juveniles attack; when intruders are very large, adults tend to flee while juveniles tend to display or attack (Figure 1). The juvenile aggression curve is virtually the same in the wet and the dry season.

4. Juvenile prey size distribution curves show a more pronounced relationship between lizard size and insect size than do the prey size distributions of the adults. Small juveniles tend to eat much smaller prey than do larger juveniles. The competition curve constructed on the basis of these prey size distributions shows minimal competition between juveniles of very disparate sizes. Yet juveniles are more aggressive toward very large and very small intruders (with whom there should be minimal prey size overlap) than are the adults with more prey size overlaps. Competition curves for the wet and dry season are very similar for juveniles.

Other results of research in the laboratory and field include the following:

1. Juveniles were encouraged to set up home ranges in captivity and these home ranges were of comparable size to those in the field. Initially juveniles were given a surplus of food, then food was removed for a period, then food was replaced. Results from experiments with eight animals and with four animals indicate that there is a significant increase in home range size when food is removed, and home ranges return to the original sizes when food is replaced. Interestingly, aggression increases significantly when food is removed and stays at high levels after the food is replaced. Aggression continues at high levels after food replacement for as much as two weeks.

2. Weekly sweep samples were compared with lizard gut contents to determine what proportion of the prey available that lizards were taking. Preliminary results from the dry season indicate that lizards take nearly all prey in the same proportion as it occurs in the sweep samples, but ants are more abundant in the habitat than they are in lizard guts.

Comments:

The high aggressiveness of juveniles relative to adults, the high frequency of aggressive displays given by juveniles, the complexity of juvenile social systems and the early display stereotypy of Anolis displays suggests that aggressive behavior is at least as important in juveniles as it is in adults. If Anolis aeneus has high juvenile mortality, a concave survivorship curve and mortality dependent on social behavior, then it is possible that the stereotyped displays given by Anolis aeneus may have evolved their present form because of selection in juvenile rather than adult habitats.

Evidence seems to be accumulating that food is not the primary reason for defense of juvenile home ranges and general juvenile aggression. Both in the wet and dry season, competition curves based on prey sizes taken predict little aggression between animals of disparate size; in fact, juveniles are very aggressive toward very large or very small intruders. A drastic decrease in food supply can increase home range sizes and increase aggression, but when food is replaced home ranges return to normal while aggression does not. It will require more experiments before we can interpret these results; one possibility is that juvenile aggression has to be "activated" by a period of food shortage. Field tests of aggression in areas with a constant high level of food (e.g. garbage piles) would be advisable here. At any rate, aggression in juveniles in both the wet and dry season indicates that food is superabundant in neither season.

Current and planned research continues to center on juvenile behavior. We plan laboratory experiments to follow up on our initial results on food manipulation, and field studies to look at the effects of habitat topography and food supply on variation in social system. Long term monitoring of a selected study area may help us determine if juvenile aggression helps the juvenile attain a suitable territory when adult.

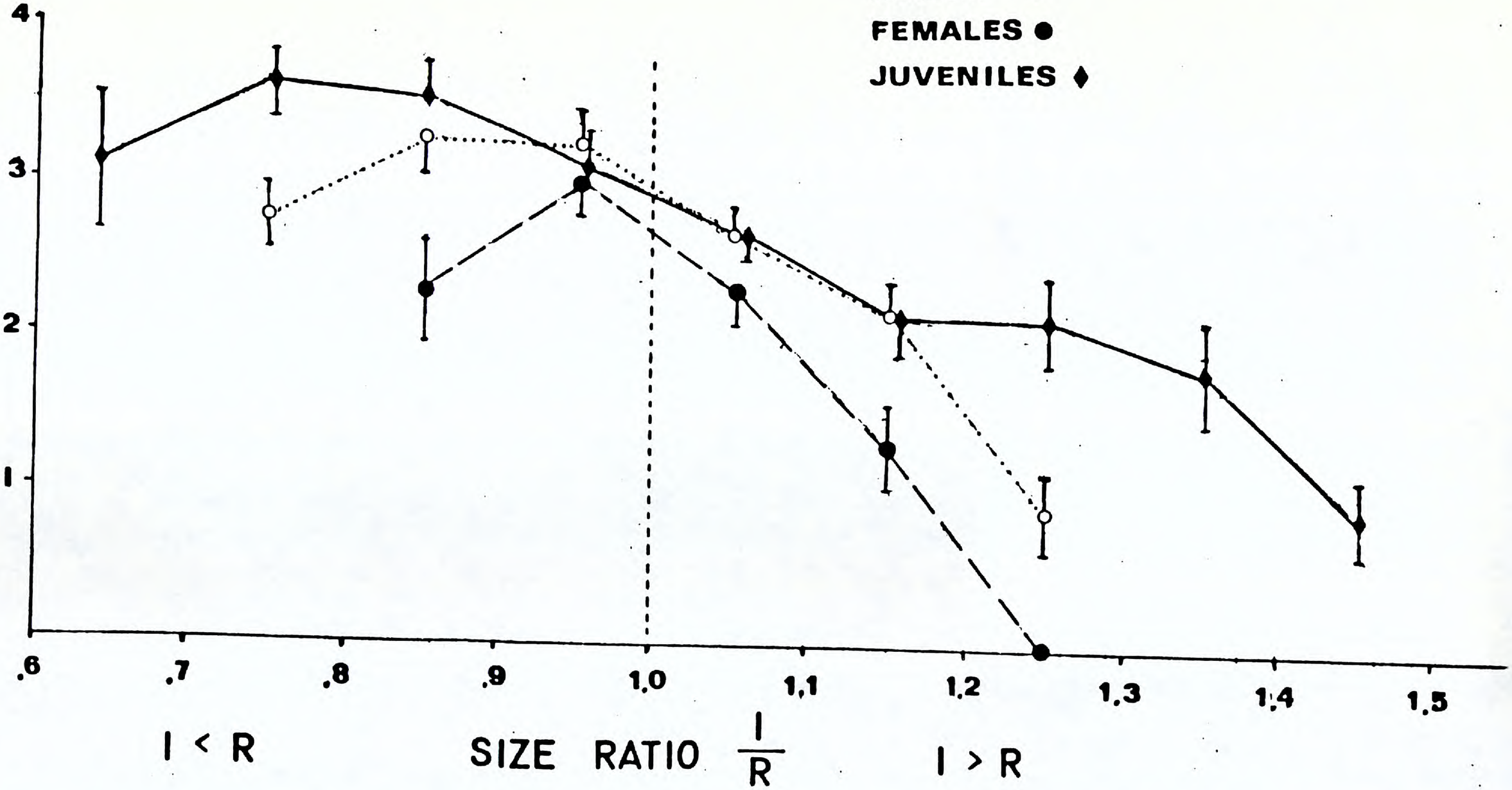


Figure 1. Actual mean aggression (± SE) based on numerical values of responses as a function of the size ratio of intruders and residents. Numbers near data points indicate sample sizes.

T. PRESTON WEBSTER, shortly before his death, turned in a draft report for the Newsletter. In it he refers to two manuscripts which, unhappily, he never finished. The expanded report below combines his last report with data from an earlier report to the National Science Foundation and certain information from the manuscripts:

Webster continued his work with the Anolis distichus species group in Hispaniola and the Bahamas, using starch gel electrophores. This project of several years standing was already of considerable maturity, and the work of the year primarily filled in holes in a story mostly already known. New material was provided by Bradford Lister, Vincent Brock, William Haas, and the Huey, Hertz, Holt, Williams expedition to Hispaniola.

The new material allowed Webster to finish his study of A. brevirostris. Supplementary information was obtained for the part of the Haitian distribution treated by Webster and Burns (1973). The northernmost sample of the taxon there designated Species B was previously represented by a small sample which has now been doubled without affecting the original conclusions. A sample collected from the hiatus between Species B and Species C is unequivocally Species A, an unexpected anomaly that Webster prefers to attribute to recent human introduction. The habitat is a stand of young roadside mahogany trees bounded in part by cane fields. The low level of genic heterozygosity in this population is compatible with its presumed youth and origin.

With two samples obtained by Huey et al., Webster has finished his survey of brevirostris from the Dominican Republic. All areas of known species abundance are represented, and despite some striking external differences, e.g. in dewlap color, all samples appear to be conspecific and best associated with Haitian Species C.

Of the many named races of A. distichus, A. d. ravitergum has received particular emphasis in Webster's research. Much of its distribution in arid areas of the Dominican Republic is bounded by populations of A. brevirostris. However, to the north and east of Bani, the distribution of these two forms is complicated by a third, A. d. ignigularis. Evidence from several populations now indicates that the two races of A. distichus intergrade in a relatively narrow zone. Samples have been examined for both morphological and protein characters with the typical variants of each race being in one case equally represented (vicinity of Rio Nizao), in another predominantly ignigularis (Jimani on El Recodo Road), in another (Matadero Road) predominantly ravitergum.

Three subspecies of Bahaman A. distichus, including the distinctive A. d. ocior with its handsome white stripe, have been examined, and with A. d. floridanus from Florida they cannot be distinguished from a single excursion of A. distichus from the source area, Hispaniola.

An investigation of proteins in a sample of a population believed to be A. distichus dominicensis from Miami has demonstrated that this population is indeed essentially identical to Hispaniolan A. d. dominicensis, as previously concluded from its morphology. It is evidently of North Island origin.

Webster continued work also on the previously reported hybrids of Anolis brevirostris (species C of Webster and Burns, 1973) and Anolis distichus ravitergum in two areas of the Valle de Neiba of the Dominican Republic 45 kms apart.

Some additional electrophoretic evidence, including I values (Nei, 1972), is available. Eight (not six) proteins are diagnostic for A. brevirostris as compared with A. distichus and the Valle de Neiba hybrids are heterozygous at the eight loci corresponding to the diagnostic polypeptides.

Examination of chromosomes in testis tissue of 37 males from the Valle de Neiba (12 A. brevirostris, 19 hybrids, and 6 A. d. ravitergum) showed that the two parental species have similar karyotypes. That of A. d. ravitergum appears to be identical to that of other A. distichus (Gorman and Atkins, 1969), while A. brevirostris differs in the morphology of one of the smaller macrochromosomes (chromosome 7 is acrocentric rather than metacentric) and in the presence (at least at Balneario la Zurza) of a variable number of supernumeraries. From none to three supernumeraries were observed per individual, producing a range of male diploid numbers from 33 to 36. The supernumeraries are comparable in size to the autosomal microchromosomes but do not invariably form bivalents during meiosis. During diakinesis in both species, the five large macrobivalents have two or more chiasmata.

Meiosis in the hybrids is disturbed. The sex trivalent almost never forms during the prophase of the first division, and a variable number of macro- and microchromosomes are represented as univalents at the first meiotic metaphase. Associations of three or more chromosomes are fairly common, and presumably some bivalents are heterologous. The first division is rarely reductional, so that twice the expected chromosome complement is found at metaphase of the second division. The consequences of aberrant first division chromosome behavior are visible at this stage. Dicentric chromosomes are rather frequent and appear to involve both homologues and non-homologues. Tricentrics are occasionally observed. As expected from the high frequency of terminal chiasmata, most dicentrics seem to be the result of crossing over close to the chromosome ends. A very few involve interstitial chiasmata and have produced visible chromosome fragments. Metacentric chromosomes with two chromated arms fused into a loop are probably the result of the same process.

Heterologous associations in the first meiotic division have been reported in hybrids between newts (Triturus cristatus, Callan and Spurway, 1951) and grasshoppers (Eyprepocnemis plorans, John and Lewis, 1965). The mechanism for such anomalies has been the subject of minor controversy (White, 1973). For the Anolis, observations on the second meiotic division demonstrate that the associations during the first meiotic prophase are chiasmatic.

The meiotic events in the hybrid Anolis can be explained by analogy to the 5 S RNA system in Xenopus laevis. A family of 5 S genes is present at the telomere of the long arm of most, if not all, of the chromosomes in the X. laevis complement (Pardue et al., 1973). During prophase of the first meiotic division, these sets of 5 S RNA genes are associated in a tight group within the nucleus. The 5 S RNA is evolutionarily conservative: for example, only 8 of 120 nucleotides differ between mammals and Xenopus (Brownlee et al., 1972). However, there is 5 S heterogeneity within X. laevis (Wegnez et al.) and the spacer sequences separating the 5 S genes are very labile (Brown and Sujimoto, 1973). It is possible that in the hybrid Anolis the similarities between families of 5 S genes are greater than between most other chromosome segments of comparable length. If the 5 S families are associated during meiotic prophase and if the pairing is generally imperfect over most of the length of a chromosome, then synapsis and crossing-over could be limited to families of repetitive DNA. Most chiasmata would be terminal and heterologous associations would be possible. In his discussion of hybrid meiosis, White (1973) suggests that heterochromatic segments may be important in the formation of irregular associations like those in the distichoid hybrids. The analogy to Xenopus 5 S DNA is simply a more specific version of that hypothesis.

[Webster had hoped to confirm the role of families of repetitive DNA in the meiotic events of his Anolis hybrids. He would have attempted to use a chromosome banding technique (especially C-banding) to determine the distribution of heterochromatin in the distichoid karyotype. He planned to explore opportunities for collaboration with a laboratory involved in the study of repetitive DNA, and then, depending on the techniques mastered and the results obtained, his studies might have been extended to include work on the distribution of repetitive DNA and chiasmata in a variety of Anolis species.

This proposed work by Webster will be followed through by a Harvard graduate student.]

On the south coast of Haiti, A. brevirostris Species C was collected at Belle Anse and Species B was taken at Marigot. Of the four proteins differentiating almost all individuals of these populations, for three (Est-1, PtE, and Trf) there is a slight sharing of variants and the data on IDH-2 for Belle Anse do not exclude the presence of the Species B variant. These results suggest introgression, at least from Species B to Species C (all three loci) and possibly in return (Est-1). The Species B variants are in low frequency in the large sample from Belle Anse, but they were detected nowhere else in Species C. The two localities are separated by

29.5 kilometers of terrain that could be explored only with some difficulty. In this area the Massif de la Selle rises abruptly from the Caribbean and A. brevirostris is apparently restricted to the vicinage of the coast. The point of contact between the two species and the extent of the suggested hybridization are completely unknown.

While the confidence intervals for estimates of genetic differentiation are substantial when only 25 loci are considered, the two contacts of Species B and C involve different levels of detected differentiation. Where there is a greater distinction (6 proteins) there is no evidence of introgressive hybridization, while on the Haitian south coast (4 proteins) there is evidence of allelic exchange.

Hybridization of Anolis brevirostris and A. distichus has been found at three localities, and at two of them it is quite common. At each locality there is an apparent lack of introgression. Such mismating may occur in at least low frequency in many if not all areas of contact between distichoid species, including those of the A. brevirostris siblings B and C. The possible novelty of the contact on the Haitian south coast is introgression, which if real is associated with less observed genic differentiation than in other contacts of distichoid species.

Webster continued work on relationships within the A. cybotes species group of Hispaniola, again from the perspective of electrophoretic examination of proteins. Material collected by Huey et al added new localities to the electrophoretic sample available for A. marcanoi, the new red-dewlapped cybotes relative described by Williams (1975). The new material confirmed the considerable electrophoretic distinctness of the taxon which morphologically is poorly differentiated (Webster, 1975).

Using material collected by Huey and Hertz, Webster has established that a population from the Oviedo-Cabo Rojo road, tentatively called longitibialis [see Haas above], is a distinct taxon with a unique set of protein variants. This evidence of differentiation indicative of species status is not surprising, as A. longitibialis is known to occur without intergradation with A. cybotes and is morphologically quite distinct from allopatric A. whitemani and A. marcanoi.

Using similar information, Webster suggests that the montane forms known as A. shrevei and A. armouri are no better than races of A. cybotes. However, each is given species status by herpetologists (e.g. Williams, Schwartz) familiar with the morphological and distributional evidence. While the issue might be solved by collecting areas of contact or intergradation, no such locality has been adequately documented Without such critical geographic data, neither A. shrevei nor A. cybotes represents a test of the occurrence of electrophoretically cryptic species within Anolis.

Webster has collaborated with Bradford Lister in the electrophoretic analysis of A. sagrei populations. Populations sampled are Jamaica (several populations), Little Cayman, Cayman Brac, Swan Id and in the Bahamas, S. Bimini, Rum Key, New Providence, and two populations on Abaco. In the last case - one population from an open area, one from forest - differences were found between neighboring populations on the same island.

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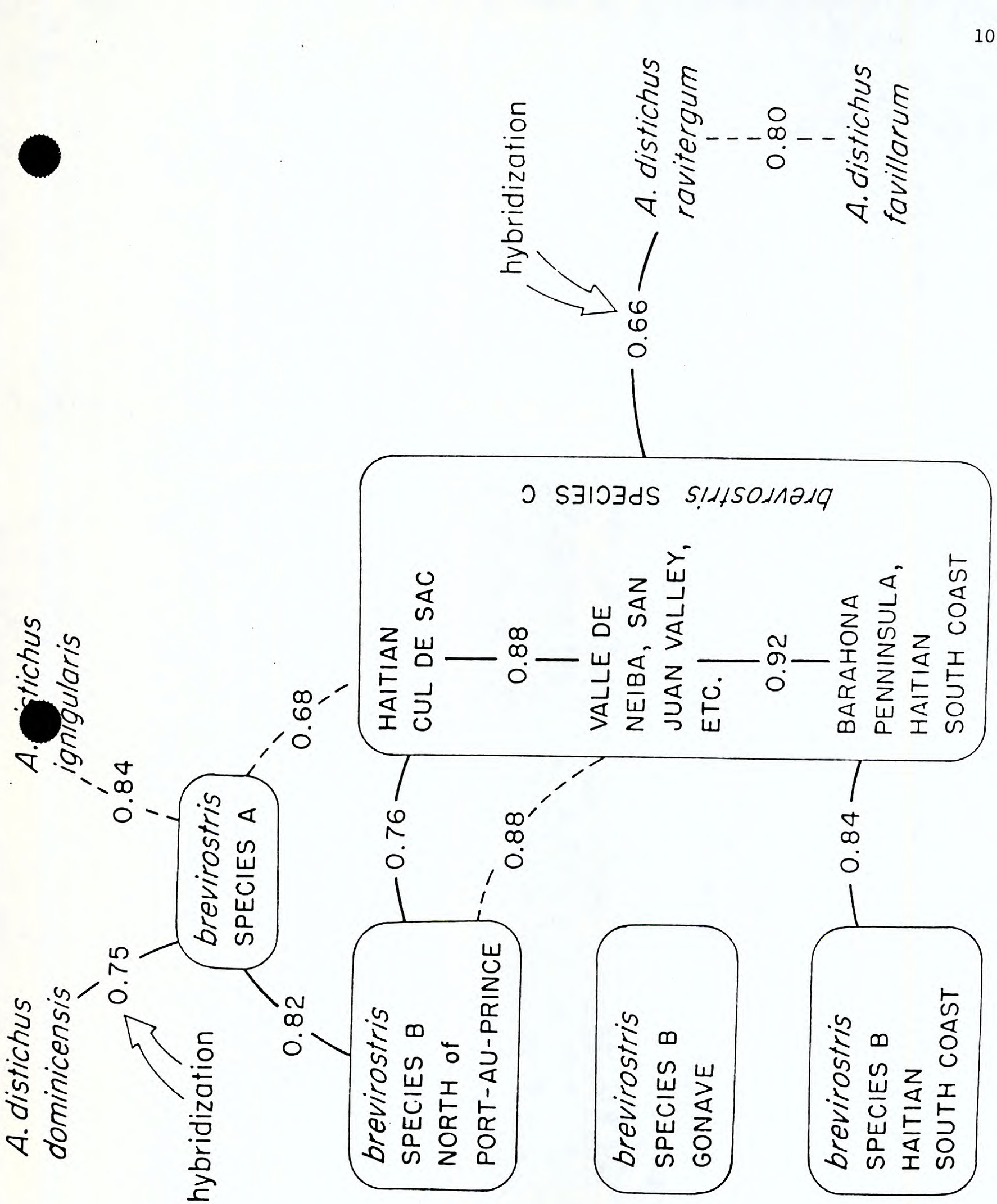

FIG. 1. I values for the brevirostris complex (and neighboring distichus).

E. E. WILLIAMS (Museum of Comparative Zoology) has involved himself in a variety of problems, most of them with some systematic aspect. He has also been concerned, at least peripherally, in a number of projects involving others (e.g. the grass anole field studies by Paul Hertz, the cybotoid studies of William Haas, the study of fuscoauratoids by P. E. Vanzolini). (See also the distichoid notes following the two incomplete papers by Webster that are informally published at the end of this Newsletter.

The problems are rather diverse and work on them is in very different stages of completion.

1. Anoles out of place: introduced anoles.

There have been a surprising number of introductions of Anolis species to areas quite remote from their natural habitat (Table 1 from Williams, in preparation). Some have not previously been reported in print; some, in fact, seem to be very recent indeed. A few can be dated more or less accurately. The interest of these should be obvious: they exhibit colonization in full process. The datable cases should be particularly interesting. To date, however, they have been little exploited. The populations on Bermuda have been more visited than the others, and two papers (Schoener, 1970; Taylor and Gorman, 1975) have resulted. Williams has seen many of the West Indian and Floridian introductions.

The several cases are cited briefly below. Williams plans a more elaborate report, fully documented and summarizing what is at present known about each example.

Anolis aeneus. This case, first reported by Kenny et al. in 1959, has been elaborately discussed by Gorman and others (e.g. Gorman and Dessauer, 1965, 1966; Gorman and Atkins, 1967, 1968, 1969; Gorman, 1968, 1969; Gorman, Licht, Dessauer and Boos, 1971; Lazell, 1972; Gorman and Boos, 1973; Gorman and Licht, 1975; Gorman and Yang, 1975) on the basis of documentation of species difference from A. trinitatis and of hybridization with the latter. Less attention has been paid to the species as a colonizer. Although preliminary observations by Holt (see above) indicate that in general aeneus in Trinidad belongs to the relatively uninteresting category of species very directly associated with man, the species is known from mangroves, and it has invaded islands satellite to Trinidad, where it shows interesting differences in habitat and abundance as compared with populations on the main island (see Holt above). In Guyana the speeies seems to be confined to cities.

A. carolinensis. In Hawaii A. carolinensis has spread within the city of Honolulu but not so far as reported significantly outside (Hunsaker and Breese, 1966). On Guam it is said to be widespread, but this is an island on which it can have but few competitors or predators. A single specimen of A. carolinensis from Half Moon Key off Belize has been discovered in a survey of the herpetofauna (Henderson and Hoevers, 1975). Since there is already a carolinensis group representative, A. allisoni (a larger species), and since Half Moon Key is an inobvious port-of-call, the presence of the species there is very surprising. There is no further information.

A. cristatellus. This Puerto Rican species is abundant in mesic gardens in the port city of La Romana in the Dominican Republic. It reaches beyond the city margin. The species appears to have been introduced along with a sugar mill built by a Puerto Rican based company during the years 1910 to 1920. Its first mention in print as a dewlap color variant of "cybotes cybotes" occurs in a paper by Chapman Grant (1956). The success of the introduction is most probably due to importation of the appropriate environment along with the lizard. The natural vegetation of the La Romana area is rather arid scrub. The abundant native anoles of the scrub - distichus and chlorocyanus - now share the more mesic habitat provided by city gardens (though they are not nearly as abundant as imported cristatellus). A. cybotes - rare in the native scrub - almost confined to relatively well-watered areas - is the native species most similar to A. cristatellus. This species is not known to occur within the city, but in one tiny area just to the east of the city where cristatellus is tapering off, it does overlap the latter species.

A. cristatellus has also been recently discovered in a park in Limon, Costa Rica. Fitch (1975) gives details. Schwartz and Thomas (1975) report it also from Biscayne Key, Dade County, Florida. Brach (1977) has studied the population.

The introduction of A. cybotes into Florida is completely documented. Lewis Ober released six Petionville specimens in the immediate vicinity of his home in northeastern Dade County (Ober, 1973). The known colony is still in the vicinity of Ober's house, but Ober reports a strong possibility that at least one other site may exist.

The Florida populations of A. distichus are discussed by Schwartz (1968) who is the principal authority on these. He considers A. distichus floridanus Smith and McCauley - formerly synonymized with Bahaman A. distichus distichus by Duellman and Schwartz (1958) and King and Krakauer (1966) - to be a valid subspecies, but possibly introduced by accidental transportation from West Andros populations.

A. equestris equestris, another species introduced from the West Indies (Cuba) into Florida, is represented by several small colonies (King and Krakauer, 1966).

A. extremus of Barbados is known from the garden area at the rear of a restaurant in Caracas (Peters and Donoso Barros, 1970). A more significant and extensive colony inhabits Ireland Island at the west end of Bermuda. The colony in St. Lucia has been looked at several times since its discovery by Underwood (1962). Gorman (1976) has given the latest observations.

A. grahami, early imported into Bermuda from Jamaica, occupies most of that island complex and overlaps marginally with extremus.

A. leachii of Antigua, the third introduced anole of Bermuda, is a larger species that has inserted itself into the center of the Bermuda range of A. grahami. The basic information on all three introduced Bermudan anoles is summarized by Wingate (1965).

A. marmoratus caryae (identification to subspecies by Lazell) is abundant within the city of Cayenne in French Guiana. Several collections have been made, but the only published report is by Hoogmoed and Lescure (1976).

A. porcatus from Cuba is known from a few square blocks in the exposition area in the western part of the city of Santo Domingo in the Dominican Republic. Though observed now for several years since first discovered by Williams and Thomas and Amy Schoener in 1970, it has appeared neither to have contracted nor expanded its minute range. A new record - a single specimen a few kilometers outside the city of Santo Domingo - was taken by Patricia Haneline in a lizard market.

A. richardi, native to Grenada, is well established in Tobago, and it is one of the cases in which importation by man is not recorded but in which the distribution of the species on Tobago (see notes by Robert Holt above) and the lack of any differentiation on this second island do arouse the suspicion that it was introduced, though presumably long ago.

A. s. sagrei is reported to have been introduced into Florida several times. Its interactions with native carolinensis deserve more attention than they have received. Its limited range within Jamaica, into which it is certainly a late invader, may mean that it was brought by man, but it is certainly old in the island. It was described there by Gosse 125 years ago.

A. sagrei ordinatus has also arrived in Florida more than once. Its history and its effects on other species again need study.

A. trinitatis, native in St. Vincent, is more local than A. aeneus on Trinidad. It may require somewhat more mesic environments (cf Gorman and Kim, 1975), but its range does seem to be constricted by competition and hybridization with A. aeneus (Gorman and Boos 1975, Holt's remarks herein).

A. wattsi on St. Lucia is very local on that island and its current status should be investigated.

Table 1

Anoles out of place

[localities in brackets indicate possible natural colonizations]

SPECIES	Area where introduced species or subspecies is native	Range of introduced populations	Date of Introduction	References
Anolis aeneus	Grenada, Grenadines	Trinidad, many disjunct populations; Guyana (cities only)	unknown, probably more than 100 years ago	Underwood 1959, 1962; Lazell 1972
carolinensis	SE United States	Hawaii	before 1950	Shaw & Breese 1951
		Guam	?	Hunsaker & Breese 1967
		Half Moon Key	?	Henderson & Hoevers 1975
cristatellus	Puerto Rico	La Romana, Dominican Republic	between 1910 and 1920	(as cybotes) Grant 1956 (cited in Table) Roughgarden 1974 Schwartz & Thomas 1975
		Limon, Costa Rica	very recent	Savage 1973; Fitch 1975; Schwartz & Thomas 1975
		Biscayne Key, Dade County, Florida	very recent	Schwartz & Thomas 1975; Brach 1977
cybotes	Hispaniola	Miami, Florida	1967	Ober, 1973
distichus dominicensis	Hispaniola	Miami, Florida	?	King & Krakauer 1966; Schwartz 1968

Anolis distichus floridanus	? W. Andros, Bahamas	Dade County, Florida	?	Smith & McCauley 1948; Duellman & Schwartz 1958; King & Krakauer 1966; Schwartz 1968
equestris equestris	Cuba	Miami, Florida	1952	King & Krakauer 1966
extremus	Barbados	Bermuda	prior to 1945	Wingate 1965
		a restaurant in Caracas, Venezuela	?	Peters & Donoso-Barros 1970
		St. Lucia	?	Underwood 1959, 1962; Gorman 1976
grahami	Jamaica	Bermuda	1905	Wingate 1965
leachii	Antigua	Bermuda	ca 1940, certainly before 1956	Wingage 1965
marmoratus	Guadeloupe	Cayenne & Bourda, a small village east of Cayenne, French Guiana	?	Hoogmoed & Lescure 1976
porcatus	Cuba	Exposition area, Sto Domingo and 5.4 km N of city, Dominican Republic	ca 1950 ?	Schwartz & Thomas 1975; P. Haneline (in press)

Anolis richardi	Grenada, Grenadines	[Tobago]	old	Underwood 1959, 1962; Lazell 1972; Holt, this report
sagrei sagrei	Cuba	S Florida	before 1931 and again in 1960 & 1964	King & Krakauer 1966; Duellman & Schwartz 1958
		[Jamaica]	before 1850	Gosse 1850; Underwood & Williams 1959; Williams 1969
sagrei ordinatus	Bahamas	S Florida	?	King & Krakauer 1966
trinitatis	St. Vincent	Trinidad	more than 100 years ago	Reinhardt & Lutken 1862; Underwood 1959, 1962; Lazell 1972; Gorman & Yang 1975 Gorman & Licht 1975
wattsi wattsi	Antigua	St. Lucia	?	Underwood 1959, 1962; Lazell 1972

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2. New terms

The heuristic value of new terms in science, particularly biological science, is a phenomenon that deserves investigation on its own, but this problem belongs in the realm of psychology. I here introduce two new terms solely on the pragmatic ground that they have sharpened my own thinking and may perhaps be of use to others.

(1) The Belem Park Effect

When I saw Amazonian forest for the first time near Belem, and then near Manaus, I was amazed not by the darkness nor the high trees but by something I did not then expect: the absence of animals. Lizards were very hard to come by in the forest, much easier at the edge or in disturbed areas. This I now know to be the common experience of those who hunt in mainland forest. I was poorly prepared partly because my major prior herpetological experience had been in the West Indies, where high lizard density, if, indeed, not universal, is the expected. But I was surprised for still another reason: just a little before this experience of true Amazonian forest, I had explored a bit of remnant forest inside the city of Belem.

Belem is now a very large city. Inside it, however, is the Bosque Municipal, a public park - not, it is true, especially overrun with people, but certainly well-used and with paths cut through and park buildings erected here and there, and a tame tapir wandering about. It is not a large park (P. E. Vanzolini estimates it at 500 m^2) but it is an island of original vegetation no longer connected with any other stretch of forest.

The lizards of the Bosque Municipal are native lizards, presumably the native lizards of the forest. Except for Gonatodes humeralis, which in parts of the park was one to several on every tree, lizard abundance was not, indeed, at best West Indian levels. Still, several Anolis punctatus and A. fuscoauratus could be seen on any visit. Mabuya mabouya and Plica umbra were also readily seen and, at the edge, Tropidurus.

The contrast with uncircumscribed Amazonian forest was vivid and unmistakable. Clearly I was confronting one of the many biological phenomena that are summed under the rubric of "island biogeography." Clearly, also, the Belem Park was more comparable to continental islands - land bridge islands - than like the oceanic islands of the West Indies.

Abundance was the feature that I saw. This is, of course, the other side of a phenomenon not so immediately obvious - extinction. There is much that is not present in the Belem Park. Some mammals and some birds are absent. Snakes were not evident; they are, I am sure, reduced in numbers and diversity. In a distinction that I like to make, Belem Park is an Extinction Island - an island in which of the two processes, colonization and extinction, the active effect process is extinction. The West Indies - classic oceanic islands - are, by contrast, islands in which the over-riding phenomenon has been colonization: they are Colonization Islands.

Holt in this Newsletter reports on mainland habitat islands, but he is dealing with introduced species, i.e., with Colonization Islands. Miyata, again, is concerned with the colonization of agricultural areas - banana and cacao groves - by forest animals. He is dealing again solely with colonization phenomena.

These are two very different processes, and it is something of a neglected fact that these two distinct processes can be distinguished and studied on mainlands.

The process of which Belem Park shows one special phase is the same upon which a large and somewhat too theoretical literature is gathering - the biogeography of nature reserves (e.g., Diamond, 1975, 1976 [the discussion following the latter]). To be stressed is the need for a vastly larger empirical base for a matter of very practical concern. What I have seen in the Belem Park needs serious study in the parks that now exist, in the park areas that are being set aside, and in the forests as they are being cut. We confront an accelerating process about which in crude fact we know very little.

(2) The vanishing refugium

This term I owe to P. E. Vanzolini but the concept is one that he and I arrived at independently from our separate vantage points of special knowledge of the West Indies and of mainland South America.

Our empirical starting point was in each case the observation that congeners, including very close relatives, often differed sharply in climatic preference. In West Indian Anolis this is a very frequent phenomenon, and the series within a species group often are climatically replacing forms interdigitating with one another in exact relation to their climatic habitats. Classic and conspicuous examples are: (1) the three grass anoles of Puerto Rico - krugi in moist, some shaded areas, pulchellus in open, drier situations, poncensis in very arid scrib, (2) the homolechis series in Cuba which ranges from allogus in deep shade to ophiolepis in open grassland. A South American example is Polychrus marmoratus and Polychrus acutirostris, the first in mesic, the second in arid areas.

There is in some of these cases absence of the obvious physiographic barriers of classic geographic speciation. One can, of course, appeal as a first suggestion to vegetational islands - refugia. Vanzolini and I have, of course, done so in our study of the Anolis chrysolepis group in South America (Vanzolini and Williams, 1972), but separation of this sort may well result in differentiation between populations but not or not necessarily in climatic differentiation.

The thought, however, has come to both of us that a simple modification of the refugium model will provide a direct mechanism for climatic differentiation. The same climatic process which fragments the original range of a

species and compresses the survivors into refugia may by intensification progressively destroy refugia. For the species survivors of these vanishing refugia there are two possibilities: local extinction or local - faster or slower - adaptation to the condition of the area surrounding their refugium. There is intense selective pressure on the local survivors; the last to survive will certainly be a very biased sample of the ecological range of the original population. If within the original population there has been the genetic potentiality for the new adaptation, it will be brought to the surface and by a genetic revolution become the new norm of the population. A climatic sibling of the original species will have been molded by the vanishment of its refugium.

This is undoubtedly only a special case of the general model of geographic speciation, but it seems an interesting and a very real possibility. Nor do we exclude the possibility that, in the transformation of the local population into the climatically distinct species, processes in addition to those proposed by the classic and simplest model of geographic speciation may have to be invoked. The "vanishing refugium" explains change in climatic adaptation, not per se, nor inevitably, speciation. (See below.)

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3. The macrosystematics of the anoles

A recent dendrogram for the family Iguanidae (Etheridge in Paull et al., 1976) provides a tentative phylogeny for the anoles and a perspective of their relationships. It is now possible to begin to place the anoline radiation in context.

Fig. 1 repeats the pertinent part of the Paull et al. dendrogram.

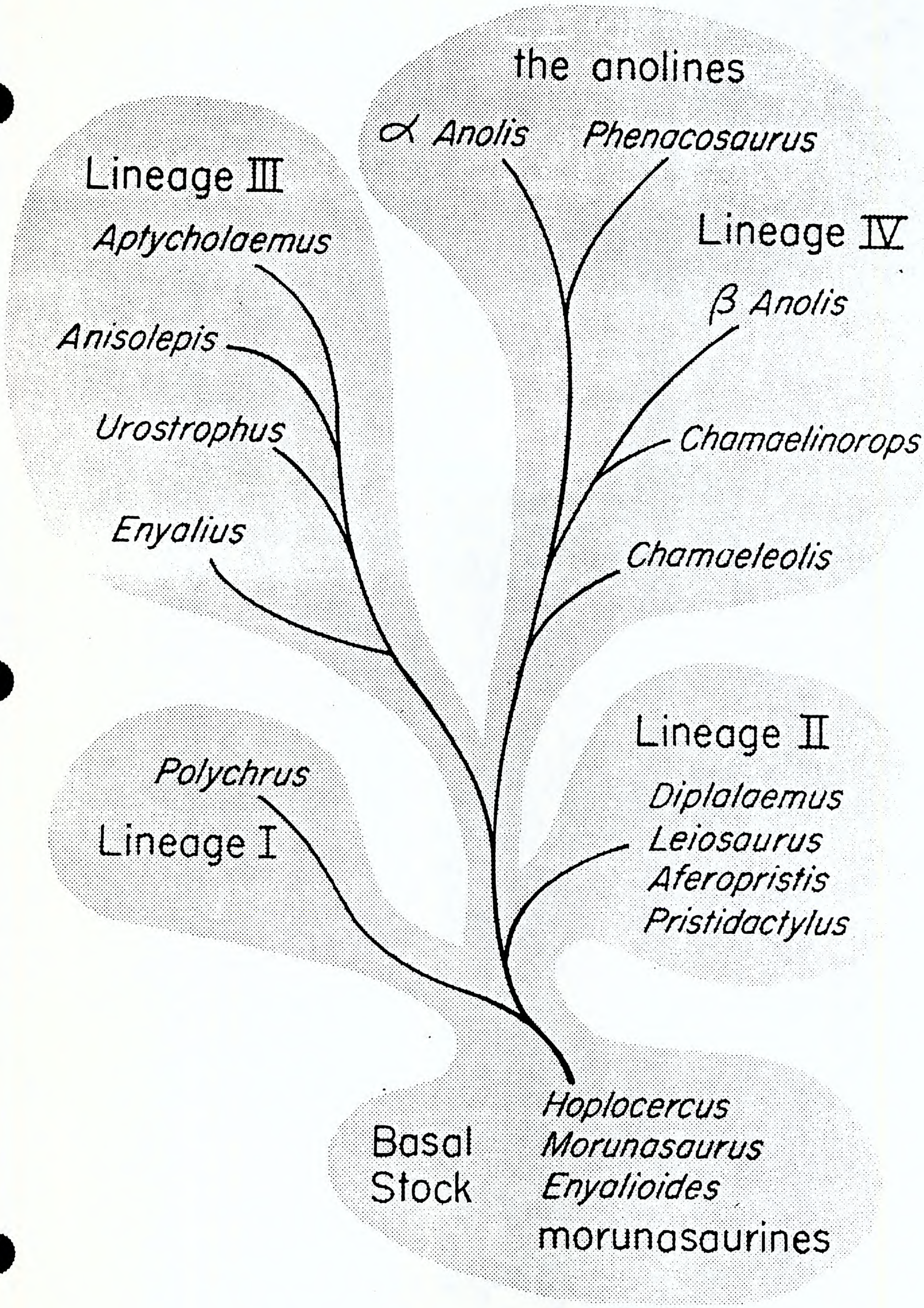
The anoles themselves are readily defined: they are iguanids primitively with expanded digital lamellae with microscopic setae plus an expansible throat fan in both sexes. No anoles are known to lack both of these features. However, some lack the throat fan altogether (e.g. the formerly recognized genus Deiroptyx with two species in Cuba) and most species have the throat fan in males only and several lineages independently show reduction in both sexes. The setose lamellae are totally lost in one species only (Anolis onca, formerly Tropidodactylus) but numbers of species independently narrow and reduce the lamellae and one specimen (Anolis annectens) is now known transitional to the extreme condition of keeled infradigital scales found in onca (Williams, 1974). Four genera of anoles are now commonly recognized. Three, Chamaeleolis (2 species), Chamaelinorops (1 species) and Phenacosaurus (3 species) are sharply distinct from one another and from the large, very variable, relatively amorphous and more highly derived genus Anolis.

Etheridge (1960) has, I think, correctly assessed the primitive characters within the anoles to be, in addition to the setose lamellae and throat fan, presence of transverse processes on all caudal vertebrae, presence of autotomy in posterior caudal vertebrae, a high number of inscriptional ribs, both pterygoid and palatine teeth, the presence of both angular and splenial in the lower jaw, an arrow-shaped interclavicle, parietal foramen between frontal and parietal. I would add as primitive a karyotype with 12 macrochromosomes and 24 microchromosomes. For each of these characters some comment is necessary.

Transverse processes on caudal vertebrae are primitive in reptiles, but only one anole has transverse processes that resemble those of other reptiles: Chamaelinorops. In this genus the caudal transverse processes are large and directed straight laterally. These caudal transverse processes differ significantly from those of the beta anoles with which Etheridge associates Chamaelinorops. The transverse processes of the beta anoles are obliquely directed forward and arise behind the transverse autotomic plane. In this combination of characters they have no parallel elsewhere and I believe them to be secondary structures - pseudodiapophyses, a hypothesis that Etheridge (1960) considered but rejected. This is an important issue which is further discussed below (see Forum). Fig. 2 compares the caudal vertebrae of Chamaelinorops, A. valencienni, A. cristatellus and A. cybotes.

The presence of autotomy planes in posterior caudal vertebrae is certainly primitive for lizards and perhaps so for reptiles (Price, 1940). A number of primitive anoles lack them, however, and since all of the highly derived species of Anolis have them, I have been tempted to consider lack of autotomy a

FIG. 1. A segment of iguanid phylogeny (after Paull et al., 1976)



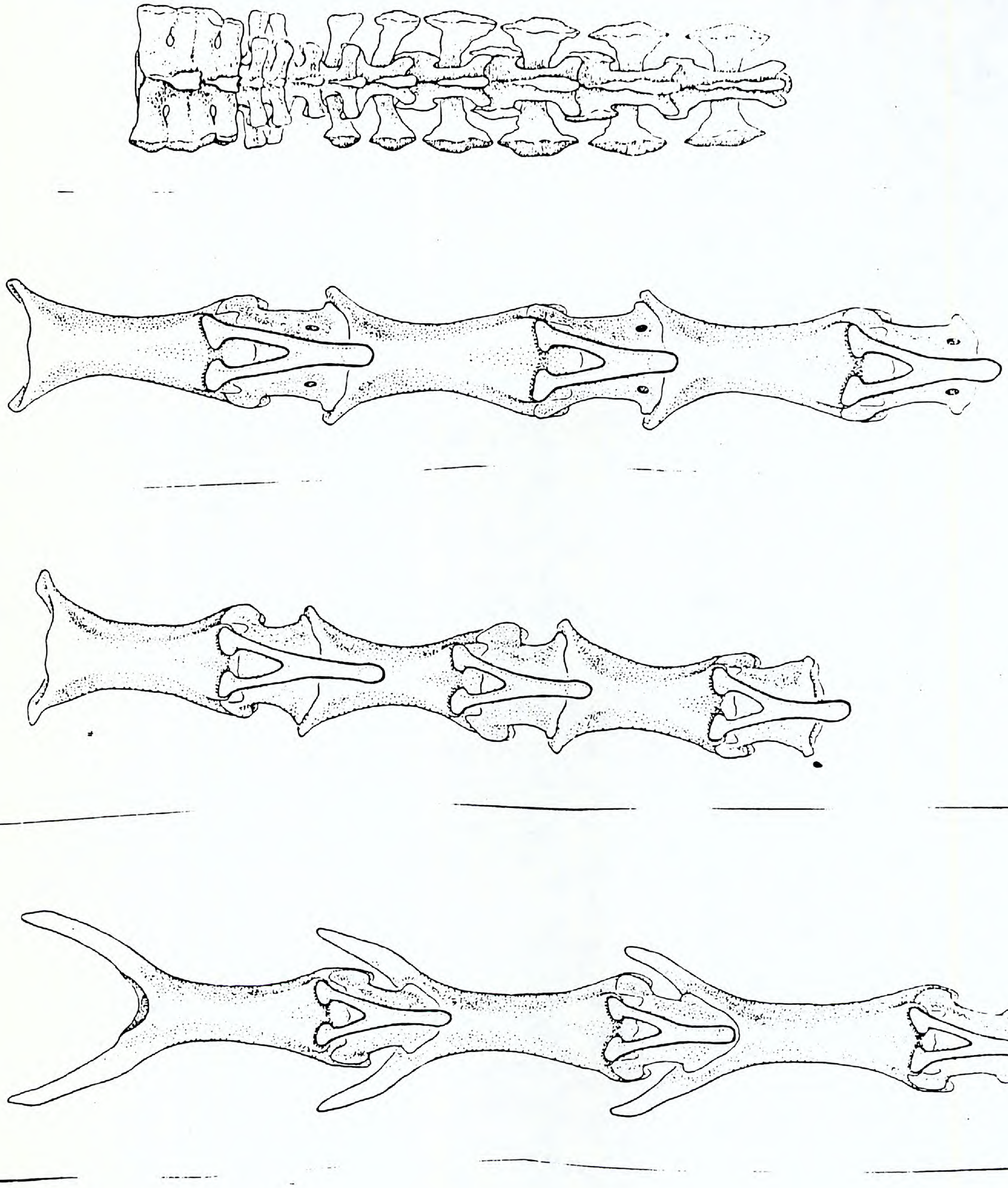


FIG. 2. Caudal of certain anolines.
Top (and in order) Chamaelinorops; Anolis cybotes; Anolis cristatellus; Anolis valencienni.

state through which all anoles passed. Etheridge's arguments on this point, however, are convincing: the lack of autotomy among many primitive anoles is not sufficiently consistent to warrant assessing it as primitive. It seems to be an alternative character several times evolved but at no time so successful that it was taken up by all anole lineages.

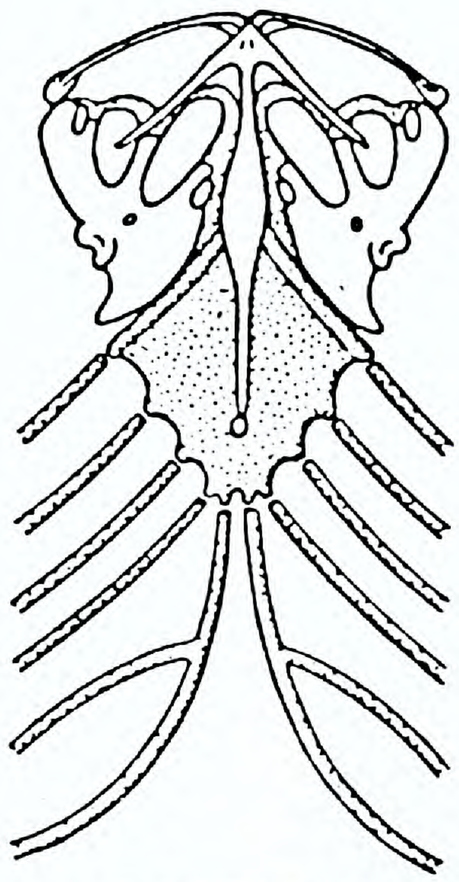
Etheridge (1960, 1965) has shown that the number of inscriptional ribs is highly characteristic of iguanid subgroups. It seems clear also that in anoles a high number of inscriptional ribs tends to be associated with characters presumed primitive on other grounds and that low numbers are characteristic of highly derived species. Chamaeleolis, Chamaelinorops and Phenacosaurus all have high inscriptional rib counts. Etheridge endeavored to erect species groups partly on the precise number and attachment of inscriptional ribs, but here his groups are sometimes at variance with evidence of very close affinities between species. It appears that reduction in inscriptional rib number and increase of number of unattached ribs has occurred multiple times and at low taxonomic levels.

The anoles tend to lose both splenial and angular in the lower jaw. Only Chamaeleolis clearly retains both. (The ventral extent of the angular in this genus is more substantial than would appear from the lateral view given in Etheridge [1960]). Both bones are absent in Chamaelinorops, but I believe this may be related to the dwarfing characteristic of the genus. The splenial is present in a number of alpha Anolis - the South American latifrons group of Etheridge ("punctatus" series of Williams, 1976) and in some of the bimaculatus group. In these it is more evident in the large species. It is present also in the Greater Antillean giants (except A. garmani).

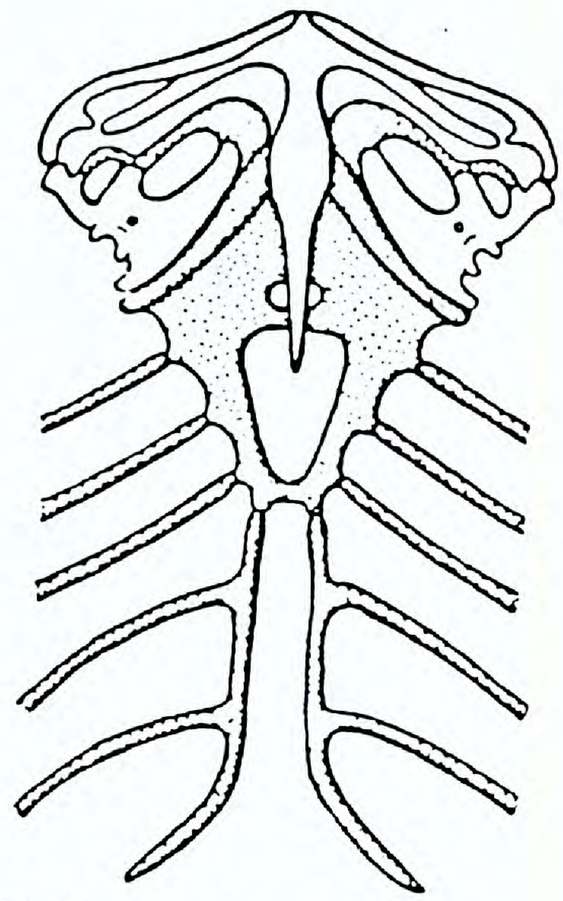
Presence of pterygoid plus palatine teeth is certainly primitive. Both are present in Chamaeleolis. Only pterygoid teeth are retained in any other anoles, again most frequently in large species.

A truly arrow-shaped interclavicle is seen in such genera as Enyaliosaurus (Etheridge, 1960). No Anolis has this extreme condition. In Phenacosaurus and Chamaeleolis it seems to be in the intermediate condition figured by Etheridge for Sceloporus and Anolis bimaculatus (Fig.3 after Etheridge, 1960). The derived extreme of a T-shaped interclavicle (arms of interclavicle in contact for their whole length with the clavicles) is seen in the carolinensis section of the alpha anoles and in the beta anoles and Chamaelinorops. The primitive lizard karyotype also occurs in all three primitive anoline genera and in some alpha Anolis but is not known to occur in any beta. (The known chromosome patterns in Anolis are summarized in a section below.)

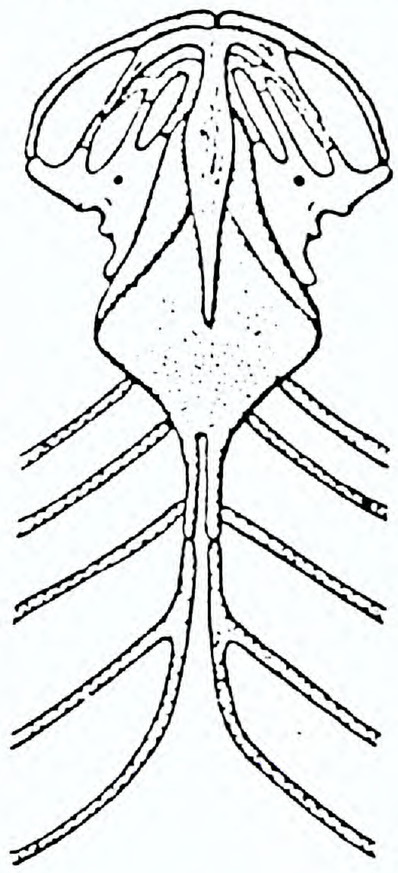
Each of the small and distinct anole genera combines primitive features with unique specializations. Chamaeleolis has a casque head so extreme that the extension of the parietals posterior to the parietal foramen is significantly greater than half the length of the remainder of the skull. Chamaelinorops has unique dorsal vertebrae with planes of bone extending between the anterior and posterior zygapophyses and overhanging normal transverse processes and rib



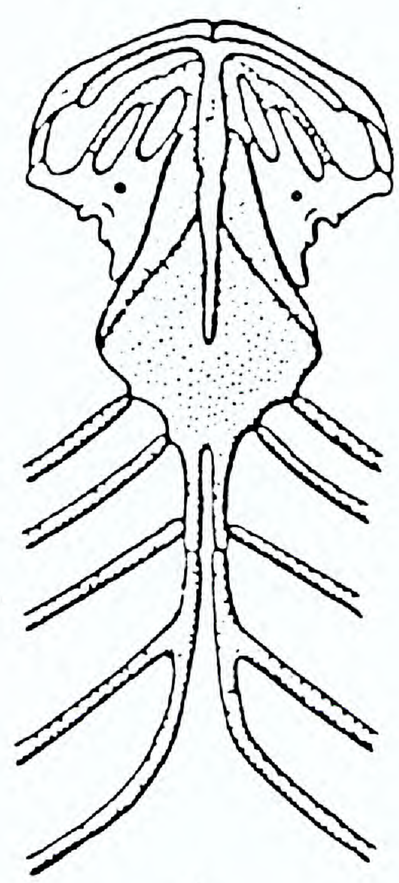
Enyaliosaurus



Sceloporus



Anolis
bimaculatus



Anolis
carolinensis

FIG. 3

attachments (Fig. 4). (I know of no parallel to this in any other vertebrate.) Phenacosaurus has a reduced number of sternal ribs and the digits are shortened and the digital pads are distinctive also (Lazell, 1969). The anterior process of the ilium lacks the strength of the process as seen in Anolis, but, contrary to Lazell's (1969) statement, this is true also of Chamaeleolis and Chamaelinorops.

The great variability of Anolis itself includes specializations which, while extraordinary, seem less extraordinary than these. Further, the variations that do occur are usually connected by almost insensible degrees with more primitive conditions. Some of the Antillean dwarf anoles do have very singular features. Anolis occultus uniquely has reduced the lateral exposure of the coronoid bone. The skull bosses of Anolis insolitus, the vertebral projections of Anolis sheplani are peculiar indeed. The probosces of the laevis group in South America form a series of which laevis is the least aberrant, connecting back to the species-rich and relatively primitive punctatus species group. Anolis onca, which once received generic rank, has now (as mentioned above) been joined by an intermediate to the remainder of the beta anoles.

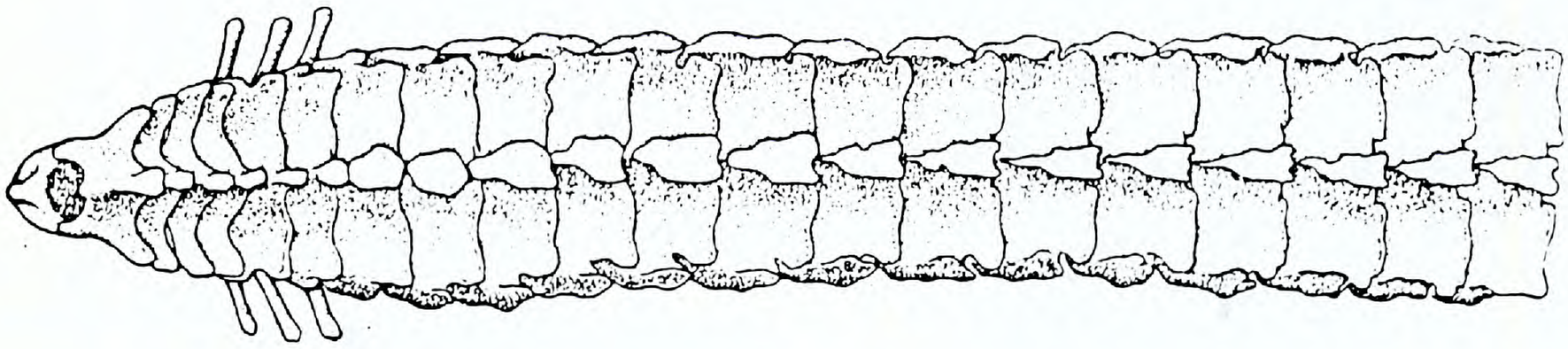
Even the beta and alpha distinction itself is compromised, at least to some degree, by the rudimentary transverse processes of the cybotes-cristatellus group (Fig. 2). As Etheridge and I have both interpreted these, they are remnants of transverse processes primitively present in the alpha series but which all other surviving members have totally lost. There is obviously an alternative view: that they are rudiments of beta transverse processes which have come to full flower in the true betas of Jamaica and the mainland.

But lest someone relate this last hypothesis too simplistically to the immunological evidence presented below by Shochat and Dessauer, let it be emphasized that the remnant or rudimentary transverse processes are present in both cybotes and cristatellus which, on an immunological analysis based on albumins, are not closely related. There is a problem here, not a solution.

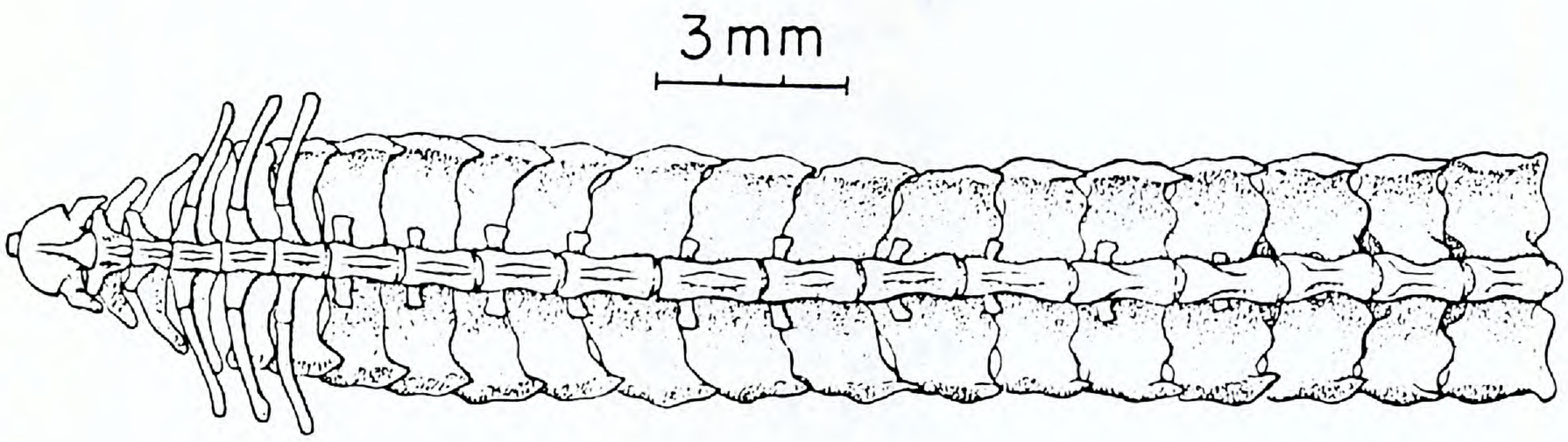
My own views of the relationships of anoles are shown in Fig. 5. They do show beta and alpha anoles as relatively closely related one to another. On Etheridge's dendrogram it is clear that the two groups should not be in the same genus: Norops should be recognized for the betas as Savage (1973) has suggested. My own position is that separation is not yet warranted by any sufficiently impressive evidence. In fact, Shochat and Dessauer's data (herein, see "Forum") call in question the validity of the alpha and beta distinction in any sense. (But see my cautionary comments following the Shochat and Dessauer presentation.)

Despite Etheridge's discussion (1960), there is not yet a full analysis of the relationships between the anoles and the Enyalius-Aptycholaemus lineage and more distantly the Diplolaemus lineage. These lineages include the few iguanids with smooth infradigital lamellae. They also include genera with relatively high numbers of inscriptional ribs (though Polychrus now regarded as more remote has even higher inscriptional rib numbers, Etheridge 1965).

CHAMAELINOROPS



Dorsal view



Ventral view

DORSAL VERTEBRAE

FIG. 4

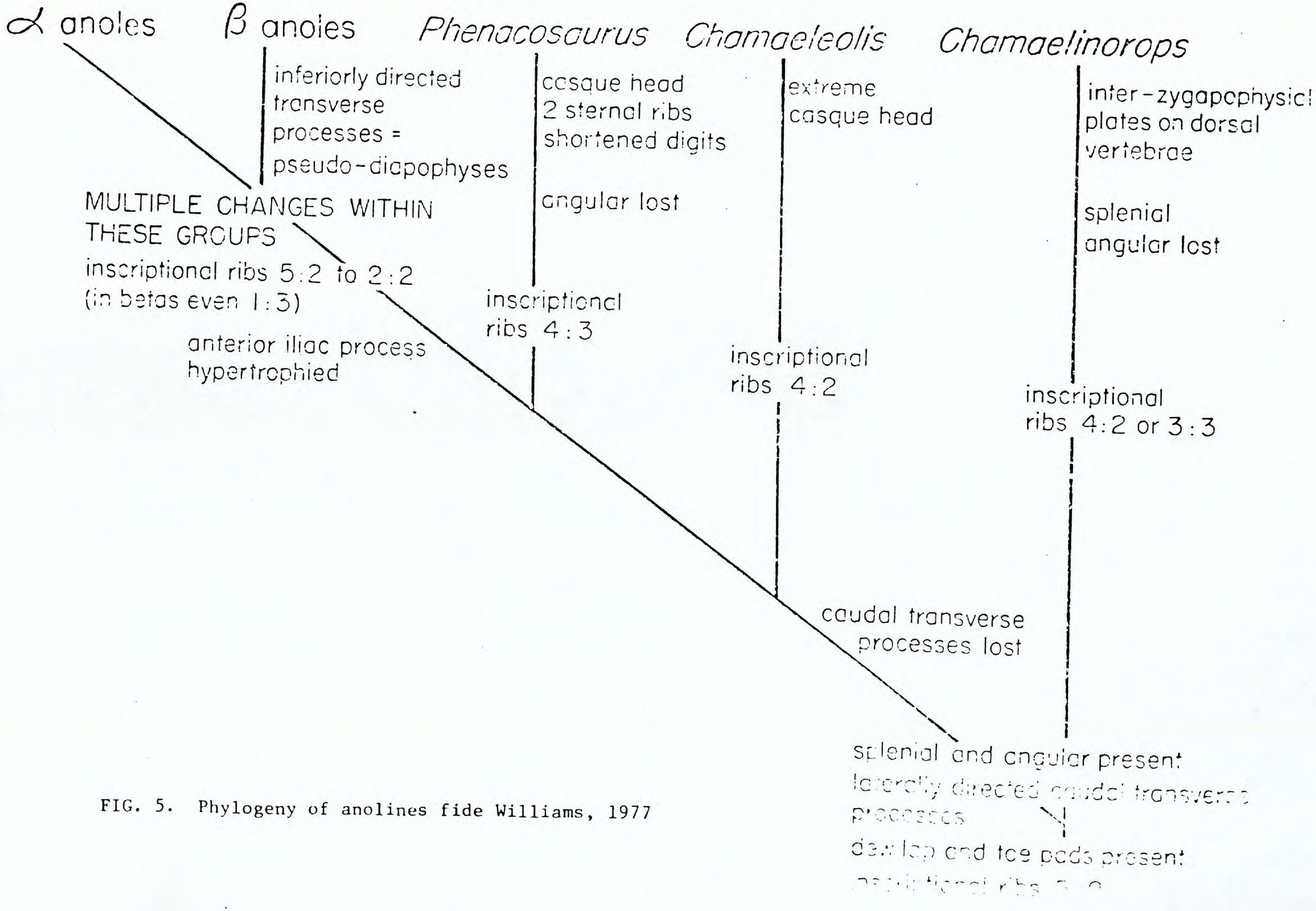


FIG. 5. Phylogeny of anolines fide Williams, 1977

All these supposed anole-related genera are in any case rather poorly known. The multifaceted methods of study employed for Anolis have not been used. (But see Cei and Castro, 1975, on serology of Cupriguanus [= Pristidactylus], Diplolaemus and Leiosaurus.) All the new techniques plus the old (osteology, internal morphology) need to be used before we can be very confident even of the generic differences between, ↓ much less the relationships of, these animals. They are an untapped treasure trove.

Even in the anoles, even in Anolis, there is much to do. The three distinctive anole genera need to be sampled immunologically, electrophoretically - even as mentioned, the osteology needs more detailed study. (This has now begun.) The karyotypes of these genera have been studied (Gorman, Huey and Williams, 1969; Paull et al., 1976) but chromosomal infrastructure is still to do. None are inaccessible, although Chamaeleolis remains more difficult than the others, not only for political reasons but because it is not known to be abundant anywhere.

The mainland Anolis begin to be worked on but are far behind the West Indian (in part for reasons I have made clear above). They are critical for our knowledge of the macrosystematics of the anoles; they need to be studied in every possible way.

↓ Curiously the two genera most often regarded as doubtful are at least readily separable on a scale character. Aptycholaemus has a transverse zone of minute gular scales associated with a gular fold. Both are lacking in Anisolepis which in appearance and habitus is very similar.

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4. Species problems

Since species descriptions per se cannot be of general interest, to represent this portion of my work I present a discussion loosely held together by the general concept of species:

(1) Problems of species discovery and description

Species descriptions are as necessary as any other kind of presentation of data. They depend - as data gathering usually does - more upon experience and familiarity with a taxonomic group than on intellectual skills. But while the description itself may be routine in form and arid in content, the discussion and interpretation should not be so. Every species description should be a mini-essay in classification and these essays will necessarily be very different in style and content. In Anolis this point has been brought home to me very vividly by my attempts to make sense of Anolis in two very different contexts - the West Indian archipelago and the South American mainland.

I have in the past few years described both new mainland species and new species in the West Indies. The papers dealing with the two areas are very different in the kinds of information involved and the security of the results.

G. S. Myers (1952) - in a paper not well enough known - has described a species description as a prediction: i.e. we are using a sample, large or small, to predict a biological phenomenon in nature. Said in this way two problems are emphasized: the problem of (1) the adequacy of the sample and (2) the validity of unstated assumptions that underlie any description. In the light of these two considerations let us compare West Indian and mainland species of anoles.

Sample size. With scattered exceptions on both sides, West Indian species are represented by larger samples than mainland species. On the mainland only after extended periods of collection, sometimes years, will substantial samples of species be obtained. In the West Indies most species may be collected in almost any desired numbers in periods ranging from hours to days. Except for the very cryptic dwarf twig anoles, this is as true of most of the recently discovered local West Indian species as of the long known widespread species. Local abundance of three to five species is usual in the West Indies. It is the experience of all collectors that abundance of at most one or two species is the mainland pattern. Even when this is said, abundance is usually measured on different scales in the West Indies and on the mainland. To one accustomed to West Indian opportunities for collection or study, the statement by one very competent mainland collector that six specimens an hour was a good catch is a cause for dismay or disgust. Some mainland species and areas do do better than this, but it is not usual, while the reverse is quite the pattern in the West Indies.

It is true that in the West Indies there are many stretches of apparently favorable territory that at least at some particular moment seem anole-less. Sometimes it may be a matter of weather or of time of day; sometimes it appears

to be real. Neither in the West Indies nor anywhere else are anoles spread at an even density over the landscape. However, when in the West Indies anoles are found, it is ordinarily in impressive density.

There are also some West Indian species that are still known from one or very few specimens. Anolis darlingtoni is a very distinctive Hispaniolan species still known only from the type. But no one since Darlington has been back to the region where the type was collected. Anolis fowleri, large and recently discovered, is known from only seven specimens although there has been some recent search for it. These are very much the exception.

Five West Indian anoles, including fowleri, have been described by Schwartz or myself or students since 1974. The smallest type series other than that of fowleri is A. sheplani (16). A. rupinae, from a logistically difficult area, is represented by a series of 22. A. marcanoi has more than 100; A. alumina more than 60.

In the same period I have described six species of South American anoles: five are based on unique specimens; one has a series of four. Worse than this, I have on my shelves 17 species I believe to be new, only two represented by series greater than two.

In the case of marcanoi and rupinae, the original samples were respectively one and two. It was necessary, however, only to go back to the correct area to obtain adequate series. In contrast, A. annectens (with imprecise locality, but the original locality for marcanoi was hardly better) has been the object of search by two field parties with a total lack of success. Six specimens of Anolis proboscis are known with relatively precise locality. Visits to the area by Anolis workers have produced nothing.

The difficulties in sampling mainland anoles are not surprising. Miyata (see above) has found that the rarer species at Centro Cientifico Rio Palenque are seen perhaps once or twice a month. One only of these is new. Clearly it is not worthwhile in South America- as it may be in the West Indies - to make search for newly discovered species a major part of any field effort. One can only put oneself in the region for other reasons and wait on the lottery of casual collecting.

Range. In the West Indies species range can be defined with moderate precision. It is even possible to say when a species is absent with considerable confidence. The ranges of many mainland species are vastly greater. With rarer species we cannot tell whether they are, or are not, very local species, such as we are now discovering in the West Indies. Species known from one or two specimens do not have a known range. We barely know that they exist.

Ecomorphs. The commoner species of the Greater Antilles fit very neatly into certain ecological categories that I (1972) have called ecomorphs. Each ecomorph has a characteristic perch, characteristic foraging behavior, characteristic escape behavior, and, associated with these, morphological and color characters that are equally diagnostic. Despite the fact that several

lineages are involved and that therefore the adaptive characters of each ecomorph must have evolved independently in each of the lineages; crown-giant, twig-dwarf, trunk-crown, trunk-ground anoles are recognizable on each of the four Greater Antillean islands and grass-bush anoles on three of them. In each case habitat, shape, color and behavior are strongly correlated, and any one of these predicts the others (Rand and Williams, 1969).

This is true of the commoner Greater Antillean anoles; it is not true of all. It is not true or not consistently true for the vermiculatus and lucius species groups in Cuba or the monticola species group in Hispaniola. Shape here does not readily predict habitat or habits. But despite these specialist species, the pattern of adaptation I have described does seem to be the "main sequence" in the ecological adaptations of Greater Antillean anoles. There even seems to be, as I suggested in 1972, a logical (perhaps obligatory) temporal sequence to these ecological patterns occurring as part of the faunal build-up and adaptive radiation of the Greater Antillean anoles.

It is quite clear that the West Indian set of ecomorphs does not extend to the mainland. It is true that such a high crown anole as A. biporcatus is green, has relatively short limbs, a high number of toe lamellae and is nearly comparable in size to West Indian giants. But this short-headed, stockily built anole is, in shape, unlike either the West Indian crown-giants or the West Indian trunk-crown anoles. The frenatus group of mainland giants are (Scott et al., 1976) behaviorally trunk-ground anoles. Some predictions can probably be made from the structure of mainland anoles. A. mirus (Williams, 1963), known as a unique and portrayed by the artist (without my authority) on a horizontal rock substrate, has narrow Norops-type toe pads and may really be a ground anole or characteristic of low vegetation; it is very unlikely to be highly arboreal. In this regard as in other features of mainland anoles, some of the adaptations are the same - presumably because there are few other mechanically adaptive possibilities open to anoles; but there are not on the mainland the strong correlations and neatly discrete ecomorphs that are so characteristic of West Indian anoles.

It is sufficiently clear from all this that the evolutionary patterns on the mainland and the islands have been quite different. It is clear that mainland anoles are intrinsically more difficult to describe and to analyze than the West Indian species. One works with the West Indian animals in the field and goes back to the field when there is another question to ask. For many mainland species no such possibility exists: their study is a museum operation, not in method or material different from that of the 19th century, and it has the classic insecurities that are inevitable in museum studies of inadequate material.

But even in the West Indies simple questions often cannot have a simple answer.

(2) "How many species?"

"How many species?" is the first and often the only question an outsider asks a systematist.

A simple question, but its very simplicity carries an assumption: that there is a simple answer. Discover, describe, count. The expectation of the questioner is that the systematist, when he has done his job, can provide a number, and if he can also give information on relative abundance, he has done more than his job.

Once I too believed that a simple count of species was, in most cases, possible. Now I am no longer sure. I come to this position from both the cases that I personally know (Anolis) and the many local and cryptic species or sibling species or species that have recently been discovered, whether discovered just by more thorough and careful collecting or discovered by karyotyping or electrophoresis.

Any realistic species map in a systematic paper is a series of dots which represent samples and which may or may not imply that the intervening area is untenanted by species. Every systematist knows that statements about the populations between samples are extrapolations, i.e. guesses. Any extrapolation may be an informed guess or an uninformed one. The systematist may know from his own field observation or that of others that populations appear to be effectively continuous across the intervening area. There may not be enough visible change between two samples to warrant any assumption of biological change. But every systematist knows of gaps in information in instances in which known change is enough to make inferences to a greater or lesser degree unsafe and judgments subjective. This is a hazard that has always existed for systematists and which may be lessened by our efforts but does not disappear.

With new methods has come more information, some solutions but more problems. It is no secret, even for non-systematists, that electrophoresis and karyotyping have been new methods of this sort. In group after group, new species have been discovered and, worse, new problems as to what a species is. Ockham's razor requires us not to multiply entities without necessity. Our problem is severer: to know what our entities are, how to define and bound them.

Actually, as evolutionists the problem should not surprise us. The idea of evolution requires us to admit intermediates, and as believers, we should not be surprised to find them. Most of us have, however, taken the position of Simpson, 1960:

> "Species do evolve and almost always do so gradually. Among evolutionary species there cannot possibly be a general dichotomy between free interbreeding and no interbreeding. Every intermediate stage occurs, and there is no practically definable point in time when two infraspecific populations suddenly become separate species. Fortunately for neontologists, the majority of living populations have either definitely passed that hypothetical point or are not yet close to it."

Perhaps most neontologists still believe this. But I do not know how anyone can talk about "the majority of living populations" in the way in which firm belief in Simpson's proposition demands. The vast majority of living populations have not been investigated in depth, nor is it clear when they will be. It is all too probable that the "good fortune" of neontologists is not a reality but a fond and foolish hope.

This has a practical, even academic consequence. A graduate student asks me how many species of Anolis there are in Cuba. I can answer this in one of two ways. I can recite the number of species names given in the most recent checklist. Or I can answer "I do not know. There are still undiscovered populations that may be of specific rank. There are currently recognized species that may turn out to be two or more. There may be some recognized species that will turn out to be in full genetic contact with other currently recognized species. There are certain also to be some populations which it will be a matter of subjective judgment and personal bias whether to put on the species or infraspecific side of some imaginary dividing line. If you are interested in numbers only, I can only give you a number which is certain to be in error. I have no means of knowing the extent of the error and perhaps not its direction."

The graduate student will by now have hurried away to some more confident authority. Yet this last is the only honest answer and therefore the only useful one. It is important that we know the fragility of our evidence.

Yet species are the cornerstone of our biology. If we do not know our species, some or much of the ground is cut out from under our feet.

One example: Fig. 2 in MacArthur and Wilson's 1967 "The Theory of Island Biogeography" is "the area-species curve of the West Indian herpetofauna (amphibians and reptiles)." The data is taken from Darlington, 1957, p. 483, who says his Table 15 is "compiled from sources cited in reference list at end of chapter." A check of the latter shows that his major source is Barbour, 1937. Darlington's data, therefore, was at least 20 years old when he cited it. It was 10 years older when MacArthur and Wilson used it.

It would not be unfair to compare Barbour's Third List with one that has just appeared (Schwartz and Thomas, 1975). But for Anolis it suffices to compare somewhat more recent lists with the most recent one. Table 1 compares Anolis in Cochran's 1941 "Herpetology of Hispaniola" with the additions since her publication. Table 2 compares Ruibal's 1964 Cuban checklist with a list of additions already known to represent less than the reality.

I knew in 1957 that Darlington's data was out of date. I was therefore quite aware in 1967 that MacArthur and Wilson's figure was unrealistic. I have never complained about the figure, however, for two reasons: (1) I could have provided more current data but not complete data. We still cannot. (2) The most important point made, that there is an area effect, is true:

TABLE 1

HISPANIOLA

Species recognized by Cochran 1941	Additions to 1976
1. armouri (as Audantia)	1. aliniger (chlorocyanus)
2. baharucoensis	2. alumina (semilineatus)
3. chlorocyanus	3. altavelensis (distichus)
4. coelestinus	4. baleatus (ricordii)
5. cybotes	5. barahonae (ricordii)
6. darlingtoni (as Xiphocercus)	6. brevirostris (distichus)
7. distichus	7. caudalis (distichus)
8. etheridgei (as A. darlingtoni)	8. christophei
9. hendersoni	9. dolichocephalus (hendersoni)
10. monticola	10. fowleri
11. olssoni	11. insolitus
12. ricordii	12. koopmani
13. semilineatus	13. longitibialis (cybotes)
14. shrevei (as Audantia)	14. marcanoi
	15. rimarum
	16. rupinae
	17. sheplani
	18. singularis
	19. whitemani (cybotes)
	+ "brevirostris species A"

TABLE 2

CUBA

Species recognized by Ruibal 1964	Additions to 1976
1. ahli	1. baracoae (equestris)
2. allisoni	2. bremeri (sagrei)
3. allogus	3. centralis (argillaceus)
4. alutaceus	4. clivicola (alutaceus)
5. angusticeps	5. cupeyalensis (cyanopleurus)
6. argenteolus	6. fugitivus
7. argillaceus	7. juangundlachi
8. bartschi	8. jubar (homolechis)
9. cyanopleurus	9. luteogularis (equestris)
10. equestris	10. mimus (cupeyalensis)
11. homolechis	11. noblei (equestris)
12. imias	12. pigmaequestris
13. isolepis	13. quadriocellifer (homolechis)
14. loysiana	14. paternus (angusticeps)
15. lucius	15. smallwoodi (equestris)
16. mestrei	16. vanidicus (spectrum)
17. ophiolepis	
18. porcatus	
19. rubribarbus	
20. sagrei	
21. spectrum	
22. vermiculatus	

For the Greater Antilles the additions to species list are greatest for Cuba and Hispaniola, much less for Puerto Rico and Jamaica. In each of the latter islands only one new species of Anolis has been discovered since 1950.

In this case then - the species-area relation - some of the ground has collapsed under us, but not all. The difficulty is attempted precision. The calculation of an exponent "z" in a species-area curve may be an exercise in quantification undertaken too early.

This, in fact, is the caveat that I would call attention to. Calculations of diversity indices or exponents for a species-area curve are only as safe as species number, and that is not safe at all. The non-systematist wants a verified species count and is apt to be irate at the systematist for saying that it is not to be had. Unhappily there is no remedy.

Partly the increase in species number in the list of West Indian herpetofauna is simply more careful collecting, more field knowledge. The new species that are being added are most often very local species or species of special habitats. They are true discoveries; the period of discovery is not yet ended.

But this part of the story has an inevitable end. The period of discovery must terminate. However, another aspect of the addition of new species cannot in principle be corrected. Some of the species which are being added are re-evaluations of old, long known populations. New techniques, electrophoresis, karyotyping, lead to or reinforce these new evaluations. Some as well of the species that are still being discovered demand also a judgment on the part of the taxonomist that they are species. Nascent species - species in the process of differentiation - defy neat enumeration. There is a lower border to the species definition which in principle can only be arbitrary.

(3) Phase I species

Most recent discussions of species (e.g. Bush, 1975) are discussions just of mode of speciation: has it been allopatric, parapatric or sympatric? Barbara Wu has called my attention to a genetic definition of speciation: Lewontin's (1974) three sequential stages of speciation - (1) genetic divergence sufficient to "restrict severely the amount of gene exchange"; "genetic divergence sufficient to permit stable coexistence"; further divergence such that the fully separated species "have become parts of separately evolving communities with no special relationship to one another as the offspring of a common ancestor." I find it useful to categorize Lewontin's stages more formally as Phases I, II and III.

Much of ecology is now concerned with the adaptations characteristic of Phase II - the stage that Diamond (1974) has defined as ecological segregation. Our current understanding of Anolis is largely in terms of Phase II relationships. The problems here are readily recognized, easily studied and, at least in principle, solvable.

Like Simpson (above), neontologists - whatever group they study - prefer to work with species in Phases II and III. Phase I species - species in which reproductive isolation is incipient rather than complete - have long been known, but, with Simpson, most zoologists have preferred to believe that they are rare (botanists have never been similarly confident). Until recently it has been possible in most animal groups to believe in the rarity of Phase I species. Now, however, in Anolis as in certain other well-studied groups - salamanders, frogs, rodents - Phase I species begin to be obtrusive - even though it cannot be said that we are more than beginning to know our difficulties.

It is, of course, true that the problem I am calling attention to with the term Phase I species has long been recognized and has already been named more than once: e.g. allospecies, semispecies, and in some usages, sibling species. I use still another term because I would prefer to emphasize the genetic over the geographic or morphological aspects.

The multiple names imply the recognition of a need. In fact, it would obviously be useful to have some special notation that would immediately set off and make recognizable those species which have not yet achieved stable coexistence - a notation calling attention to their evolutionarily intermediate character.

In a recent paper I attempted something of this sort (Williams, 1976). In a checklist of the anoles of the West Indies, I distinguished between species that had achieved sympatry and the allopatric members of superspecies by printing the names of the describers of the species of the first category in large capitals, while leaving the names of the describers of taxa of the second category in normal type. This was an awkward effort and it is unlikely to have any imitators, even myself.

But it has seemed to me worthwhile to make this distinction. Fortunately Amadon (1966) has already suggested a much simpler way of indicating taxa intermediate at the species level - the use of brackets. Thus the giant anoles of Hispaniola are the Anolis ricordii superspecies and the allopatric or Phase I species within this complex are A. [ricordii] ricordii, A. [ricordii] baleatus and A. [ricordii] barahonae. The merit of this notation is that in a very simple way it signals several biologically interesting things: relationship, allo- or parapatry, greater or less ecological similarity and probable incomplete reproductive isolation.

For me, it will be a major merit of this convention, if it is generally adopted, that no positive statement is made about reproductive isolation. In other words, it serves a very human purpose: it permits a statement of ignorance.

Reproductive isolation, as critics of the biological species concept have long pointed out, is frequently difficult to demonstrate. For truly allopatric populations it is, of course, impossible to do so in nature. In contrast, phenetic resemblance, allo- or parapatry and ecological similarity are relatively easy to document.

In terms of reproductive isolation there is, in fact, a great grey zone between the obviously infraspecific populations that are in full genetic continuity and fully sympatric species that are ecologically segregated. Within this grey zone there is clearly a spectrum of degrees of reproductive isolation from almost complete separation to slightly diminished gene flow. The futility of attempting to partition this grey zone between species and subspecies is quite adequately proven by the acrimonious disputes of generations of taxonomists where every decision has been subjective or has been an exercise in the placement of the burden of proof. Since disputes tend to be more virulent the worse the evidence, the only solution is to recognize ignorance when that is the problem and to admit the worthlessness of partitioning when there can be no agreed upon grounds for decision. It is for this reason that I suggest that the whole grey area of species distinction be subsumed by one notation - Amadon's brackets.

Within the grey area - not in nature but as taxonomists view it - I see two conditions: (1) real intermediacy of very varied grades in reproductive isolation, (2) simple lack of information on reproductive potentiality. The intermediate conditions belong in the grey area as a matter of evolutionary reality; the cases of ignorance may be artifacts of the current level of our information or they may be (e.g. allopatric populations) intrinsically not resolvable.

I can visualize cases in which I or anyone on current evidence might use brackets that in the future proved to be full species that overlap without introgression or for others that might, by smooth intergradation, be shown to be unmistakably infraspecific. But it seems to me highly desirable to leave in the limbo of the brackets all those cases that cannot be unambiguously assigned to species or infraspecies status.

To apply this again to anoles, there is the Anolis hendersoni complex. I at one time (Williams, 1963) called the three members of the hendersoni bush-anole complex subspecies. Schwartz and Thomas believe that they have evidence of overlap. The case still needs careful re-examination in the field. I would at present use A. [hendersoni] hendersoni, A. [hendersoni] bahorucoensis and A. [hendersoni] dolichocephalus.

Still another case and one much discussed in this Newsletter: Webster and Burns discovered within the brevirostris complex in Hispaniola three allopatric populations that electrophoretically were differentiated to approximately the species level and that seemed also to show character displacement in dewlap color where their ranges adjoined. I would use brackets in this case also.

But the distichoids are a difficult problem in any system. A. distichus overlaps one member of the brevirostris superspecies with only rare hybridization and in its contact with another member of that superspecies at some places overlaps it, while in other places numbers of hybrids are regularly found at the contact zone. I personally would call A. distichus a full species as against the brevirostris superspecies, but I would not quarrel with someone who chose to write all the distichoids with [distichus] in brackets. Equivocal cases such as these can probably only be treated equivocally. Essentially the device of using brackets would have the intention of indicating for some populations that their species status was sub judice either intrinsically because they were intermediate - a Phase 1 species - or because of an informational gap.

I do not visualize brackets as being in use every time that a name for which brackets are appropriate is used. Like subgenera, the superspecies notation might be most frequently used in checklists or in discussions of species status. More commonly the same taxon would appear as a simple Linnaean binomial. In all local situations in which it coexists with species not closely related to it, the binomial is appropriate. The issue of a bracketed superspecies name should only arise when allopatric populations of the same group need to be mentioned.[1]

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[1] I reject as a perversion of Amadon's fundamentally useful suggestion of 1966 the emendation of Amadon and Short (1976, Syst. Zool. 25: 161-167). Their distinction between "megasubspecies" and "allospecies," the first to be designated by parentheses, the second by brackets, attempts to partition an area in the evolution of species which has, as I would see it, as its defining character the impossibility of clean and objective taxonomic divisions.

(4) Speciation or how do Phase I species arise?

A. The problem of intraisland speciation and radiation.

In 1972 I published a paper the theme of which was "the origin of faunas." I was able to show a striking congruence between a phylogeny of the eleven Puerto Rican Anolis and an expected sequence of ecological adaptations inferred as occurring by character displacement as each new species was added to the fauna. I treated "the origin of faunas" wholly as a problem in the coadaptation of species and took the origin of the species themselves as given.

It is true that the ecological sequence that I postulated for Puerto Rico is not dependent on the mode of origin of the coevolving species, whether they originated in situ, as I then suggested for all Puerto Rican species, i.e. by radiation within the island, or whether some of them arrived from elsewhere, i.e. by accumulation of species from other islands.

The accumulation of colonists that are already species when they arrive required only that they fit together ecologically. There have been many studies of this ecological coadjustment. The most recent and elaborate, that of Diamond (1974), sets very intriguing "assembly rules" and "incidence functions," but he again assumes full species status for the members of the communities that he studies and makes no mention of intraisland radiation.

But radiation - species formation - within one island bank clearly did occur in Puerto Rico. Perhaps not all of the anoles did originate there (recent evidence indicates that two did not), but the majority certainly did. In the 1972 paper I mentioned this problem only to dismiss it. Radiation in situ is a problem in speciation and it has long been unclear that the geography of the West Indian islands permits a solution of all cases of speciation in terms of the classical isolation of populations by physiographic barriers. For Puerto Rico I avoided the problem by declaring (1) that the issue was not germane to the evolution of ecological coadaptation that was the main theme of my paper and (2) that the Puerto Rican bank, including as it does the several Virgin Islands appeared to have sufficient complexity to permit intra-bank evolution of its fauna.

However, it has never been possible to wave away in the same fashion the problem of the origin of the six native Jamaican species. Here, more clearly than for the species of Puerto Rico, the endemic six did not come from elsewhere but did originate on the Jamaican bank. Yet on Jamaica it is far less obvious than on the Puerto Rican bank that there are geographic barriers that will serve the allopatric model of speciation. Lazell (1966) did indeed attempt to derive all Jamaican anoles by successive invasions of the mainland from a dry island seven miles off the coast, an island that would only exist in the wet phases of the Pleistocene. Such a scheme, unassisted by factors other than physiographic separation, has always seemed to me implausible. The Jamaican bank, like that of St. Vincent in the Lesser Antilles for which Yang et al. (1974) suggested a similar fringing island mechanism for speciation, has exceptionally small and close satellite islands.

Furthermore, on the island of Hispaniola, only one pair of species - the larger green anoles, A. chlorocyanus and A. coelestinus - conforms neatly in its distribution to the major physiographic barrier - a below sea level trough that divides Hispaniola into northern and southern elements. There are indeed other species which may have originated as the result of division of the ancestral population by the sea barrier, but the present distribution of the semilineatus group, for example (Williams, 1961; Hertz, 1976), has to be explained by more or less complex migrations after species origin. Some, however, of the more recently discovered species are difficult to explain in this way. Anolis marcanoi (Williams, 1975) appears to be surrounded on all sides by its sibling, A. cybotes, and it is completely inobvious what physiographic refugium could have provided its place of origin. Species A, B, and C of the A. brevirostris complex (Webster and Burns, 1973) again correspond poorly to any physiographic or ecological landmarks, and the relationship of the complex as a whole to its sibling distichus is complicated enough to require special historical explanations, or, again, other than physiographical factors. The monticola microradiation (Williams and Webster, 1974) at the extreme end of the western peninsula of Haiti again presents a picture not easily reconcilable with any simple geographic model, and in this case there are associated chromosomal peculiarities that suggest an alternative.

B. Chromosomes and anole speciation

1. What is known.

A very substantial fraction of the West Indian Anolis have now been karyotyped. There are very few species groups or subgroups in which no member has been done. Not surprisingly, all are Cuban: the argillaceus group (argillaceus, centralis, loysiana), the Cuban grass anoles (alutaceus group, nine currently recognized species) and the angusticeps subgroup (angusticeps and paternus). Very rare species have not been done, i.e. A. darlingtoni known from the unique type; A. roosevelti, still known from only two specimens; A. imias, known from only two specimens. In other cases, species now recognized had not been separated taxonomically from close relatives when the karyotyping was done (usually on one or a few specimens). It is, of course, quite likely that these newly recognized species will fit in with the remainder of their series or group when their chromosomal formula has become known. Those sibling species that have been karyotyped have thus far always had karyotypes at least grossly similar. Table 1 summarizes data on diploid number for Anolis.

Unnoticed in this table as in Gorman's (1973) account is intraspecies variation: Webster in the First Anolis Newsletter pointed out some samples. I repeat his information (the First Newsletter had minimal circulation) and add some additional examples.

(1) Polymorphism in the monticola group on the Tiburon peninsula. Webster: "A. monticola has a diploid number of 46, 47 or 48. Of 46 individuals examined, four have a diploid number of 46, one has 47, and the remainder have 48; All with numbers less than 48 are from localities at the western end of the known distribution. A number of chromosomes have undergone inversion, resulting in conversion of telocentric fission products to submetacentrics or metacentrics. The extent of fissioning is variable both between and within localities, but seems less developed at the western localities. While this situation awaits further analysis of present preparations and more collecting, it would seem that the eastern populations have become stabilized for fully fissioned karyotypes and have undergone substantial secondary modification of chromosome morphology, while the western populations are as yet not fully fissioned and have experienced less inversion." The other two Tiburon species of the monticola group are partially fissioned, A. koopmani with a 2N of 40 while A. rupinae has a 2N of 40-44. Webster reports of the latter: "Of two specimens taken at the type locality, both have 13 rather than the common twelve pairs of microchromosomes: one is homozygous for one fission, heterozygous for a second, and homozygous for four metacentric microchromosomes; the second is homozygous for two fissions, heterozygous for a third, and homozygous for three metacentrics. This suggests that within this one population diploid numbers range from 40 to 44."

(2) Anolis etheridgei shows either 12 or 13 microbivalents in meiosis.

(3) A. brevirostris (species C as reported in Webster in this Newsletter) has a variable number of supernumerary chromosomes.

(4) A. cristatellus (Gorman et al., 1968) shows supernumerary chromosomes in some populations. This has not been further investigated.

(5) A. grahami. Following a lead from Gorman, William P. Hall (1974) with Alberto Espinoza N found extraordinary complexity in this species, with diploid numbers ranging from 2N = 30 to at least 2N = 36. There were two independent phenomena: (1) occasional accessory chromosomes, (2) fissioning of at least three pairs of chromosomes. Hall and Espinoza thought there might also be considerable non-Robertsonian variation in the macrochromosomes.

The survey by Hall and Espinoza covered only about 1/3 of the island but encountered remarkable geographic variation in the fissioning, at some places a single fission fixed for this as a morph occurring with unfissioned 2n = 30, other populations fixed for two fissions and polymorphic for a third. There were possible ecological correlations with the fission patterns, but not an obvious correspondence within the ranges of the two described subspecies, A. g. grahami and A. g. aquarum. (As a further complication, Schwartz and Thomas [1975] suggest the two forms are species not subspecies, since some specimens of each have been found within the range of the other.)

(6) A. opalinus. Gorman suspected xy heteromorphism here. Hall and Espinoza report uncertainty as to whether this is the condition or a pericentric inversion of pair 7. In two localities they report supernumerary chromosomes; in one case one of three individuals had two supernumerary chromosomes, in the other one of two had a single supernumerary.

(7) A. garmani (Hall and Espinoza) shows accessory chromosomes in some populations.

(8) A. whitemani has the primitive 12 macrochromosomes plus 24 microchromosomes pattern. Webster reported (op. cit.) that in two specimens from the Dominican Republic one of the 12 pairs was greatly enlarged.

(9) A. cybotes, again always has the primitive 2N = 36 karyotype, but Webster noted that "a small proportion of individuals have the morphology of a chromosome substantially modified."

(10) A. fowleri. As reported in the last Newsletter (Webster, 1974), the single specimen of this rare species karyotyped had a diploid number of 44, but the 20 macrochromosomes do not sort into 10 pairs of morphologically identical homologues. There is considerable asynapsis in the first meiotic division and the first division is not reductional.

Actually, as regards intraspecies variation these cases represent the few species in whch karyotype variation has been seriously looked at (mostly by Webster) and it is not unjust to say that in the matter of intraspecies study of Anolis karyotypes in depth there is everything still to do.

Except for the fissioning in the monticola species group, however, there is no present evidence that this intraspecies chromosomal variation has been important in initiating speciation. At the gross level, when comparing closely related species, there appears to be more intraspecies variation than interspecies difference.

The occurrence of a conservative karyotype in many West Indian anoles - the 12 macrochromosome, 24 microchromosome pattern believed to be primitive for lizards (Paull et al., 1976) - would seem to point in a similar direction and to force the conclusion that in anoles chromosomes have not been important in speciation. It is, of course, the phenomenon of conservative karyotypes common to whole series of closely related species that has always been a stumbling block for those who would argue for the critical importance of chromosomal species. Even Hall, in Hall and Williams and Paull et al., has emphasized the contrast between rapid chromosomal speciation in such a recently evolved genus as Sceloporus with the presumably slower genic speciation of Anolis.

But is the contrast entirely valid? Gross karyotypes are not an adequate measure of species difference in chromosomes. There is an infrastructure to chromosomes - in part revealed by banding techniques, in part by studies of repetitive DNA - which is quite uninvestigated in Anolis at this time. This would seem to be a direction in which to go.

It is accordingly the major current effort at Harvard to go beyond karyotype to chromosome banding and repetitive DNA. Two new students of Anolis are carrying the primary burden of this work - Barbara Wu and Judy Blake.

These two infrastructural aspects of chromosomes will tell us some important things. Banding will be of great use in establishing chromosomal homology and also in indicating small chromosome rearrangements. It will be useful, therefore, in taxonomy and phyletics, and rearrangements may indicate some of the chromosome differences that result in meiotic dysfunction in hybridization.

TABLE 1

Chromosome Diversity within West Indian Anolis

I. The primitive karyotype, similar in gross detail, including arm length.

12 v + 24 m

most species on Cuba and Hispaniola

II. The primitive karyotype modified by loss or fusion of one pair of microchromosomes.

12 v + 22 m

III. The primitive karyotype modified by fissions.

e.g. 24 v + 24 m

the monticola group s. str., insolitus

IV. The primitive karyotype modified by complex changes - translocations, inversions - the early stages in the sequence not represented by any modern form.

A. Sex chromosomes not known

1. 14 v + 16 m - lineatopus, garmani, valencienni in Jamaica

2. 14 v + 14 m - the sagrei series in Cuba

B. An xy system evolved

1. 12 v + 2 v + 10 m + xy - evermanni (Puerto Rico)

2. 14 v + 16 m (7 pair ? = xy) - opalinus (Jamaica)

C. An x_1x_2y system evolved

1. The Puerto Rico-Northern Lesser Antillean radiation - evolution by translocation and inversion

12 v + 2 v + 12 m + x_1x_2y - stratulus (Puerto Rico)

12 v + 2 v + 14 m + x_1x_2y - acutus (St. Croix)

8 v + 6 sI + 4 v + 8 m + x_1x_2y - bimaculatus and wattsi complexes (Northern Lesser Antilles)

2. The last modified by fission of two macrochromosomes

   6 v + 6 sI + 4 v + 4 I + 8 m - x_1x_2y - oculatus (Dominica)

3. The Hispaniolan distichoid radiation

   10 v + 4 v + 16 m + x_1x_2y

   a. chromosome 7 metacentric - distichus

   b. chromosome 7 acrocentric - brevirostris species A, B and C (species C also with B chromosomes)

4. The Puerto Rican trunk-ground and grass anole radiation

   12 v + 4 v + 10 m + $x_1x_1y_2$

   cooki (Puerto Rico) and monensis (Mona); gundlachi, krugi, pulchellus, poncensis (Puerto Rico)

   The two subsets differ in the presence of a distinct break in size between the intermediate size chromosomes and the microchromosomes in the gundlachi set

5. The previous pattern modified by loss or fusion of one pair of microchromosomes

   12 v + 4 v + 8 m + x_1x_2y - cristatellus, scriptus (southern Bahamas)

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Thomas Preston Webster died before he had quite finished his thesis. He had in fact promised two theses, one on lizards and one on salamanders. He very nearly achieved that goal. His already published important and much cited work in both areas would have been included in any formal thesis, and he had been hard at work on both fronts at the time of his death. One salamander paper with Richard Highton has since appeared. On lizards, besides notes that are too incomplete or were intelligible only to himself, he left behind the texts of two manuscripts on distichoid anoles that he himself felt were in near final form. They lack, however, the tables and figures and numerical data he would have prepared to give his statements full documentations.

These two papers cannot be published formally in their incomplete state. Yet there is much information here that deserves dissemination and should be available for use by those who carry on Webster's study of distichoids. It seems wholly appropriate therefore to employ the informal vehicle of this Newsletter to present Webster's last papers essentially as they were written, including even references to missing tables and editing or emending only where it seems essential, e.g., obvious inversions of meaning, citations as manuscripts of papers that are now published or in press. (Webster's last Newsletter report above includes some of the same information. We are deliberately repetitive in the hope that as much of the information of Webster's final two years of work may be salvaged as possible.)

Geographic Variation in "Anolis brevirostris": Evidence from Proteins and a Consideration of Dewlap Color

Webster and Burns (1973) interpreted electrophoretic observations on several proteins to assign Haitian populations of the lizard Anolis brevirostris to three informal sibling species. The region sampled was selected to represent the substantial geographic variation in dewlap color known to occur not only within this species, but also within its sibling, A. distichus. The conclusion - that differences in dewlap color are available to promote reproductive isolation between the sibling species - is here re-examined with additional information from the same area and with comparable data from most of the remaining distribution of "A. brevirostris." As before, gel electrophoresis was used to study proteins and the results are interpreted as genetic relationships among populations. All new samples are referred to one of the three sibling species recognized in the Haitian study, but additional geographic differentiation in dewlap color cannot be interpreted on the same basis.

Materials and Methods

As the earlier study had found significant differentiation occurring over distances of a few kilometers, an attempt was made to continue the pattern of relatively local sampling. To keep the corresponding electrophoretic study to reasonable proportions, most samples are of modest size, with an occasional larger one to serve as a regional reference. Samples of A. brevirostris were usually collected by myself, although volunteer or paid local assistance was used at times. Samples 44 and 45 were obtained in 1974 in lizard markets run by P. E. Hertz, R. Holt, R. B. Huey and E. E. Williams.

The modal condition of the male dewlap and the range of variation were recorded after an examination of all males in a sample.

For electrophoresis, lizards were frozen in hotel freezers and transported to Cambridge on ice. The adults in most samples were dissected, with a combination of tail, leg muscle, and viscera providing the electrophoretic sample and the remainder a reference in the collection of the Museum of Comparative Zoology, Harvard University. Whole animal homogenates were prepared for juveniles and for adults in a few samples.

In general, methods of sample preparation, horizontal starch gel electrophoresis, and protein staining or assay follow Selander et al. (1971). Other methods appear in Shaw and Prasad (1970). Details for A. brevirostris have been provided in part by Webster and Burns (1973). The remainder are available on request.

The electrophoretic analysis has been modified and expanded since the first gels in 1970. The most complete results are available for recent samples, and not all of the earlier material has been re-examined to make it fully comparable. When necessary, such discrepancies will be noted in the results.

Relationship between populations is expressed as an index of genetic similarity (I, the normalized identity of genes; Nei, 1972).

Results

Sampling. Webster and Burns (1973) considered samples from 12 localities in Haiti. Their numbering is retained here. New material from the same area represents locality 4 and a locality intermediate between 7 and 8, locality 7'. With the exception of the interior of the San Juan Valley in the Dominican Republic and isolated populations on Haiti's Tiburon Peninsula, all of the distribution on Hispaniola is included (Figure 1, Table 1). A single sample was obtained on the Ile de la Gonave, but no material is available from Isla Beata.

Dewlap color. As previously reported, the pattern of geographic variation over the sequence of population 1 to 12 includes two strong contrasts, between localities 3 and 4 and between 7 and 8. The additional sample from locality 4 matched the earlier observation of typically pale dewlaps. Males at locality 7' are indistinguishable from males at localities 1 through 3, where the dewlap skin is completely orange.

Elsewhere on Hispaniola the range in dewlap color is great, from grey at locality 40 to red orange at 28 to pale monochromatic at 44 (Table 2). In addition, the variation in dewlap color within a sample (e.g., 36, 43) can be considerable. There are three areas of fairly dramatic transition. In the Valle de Neiba, over the 33 kilometers separating localities 17 and 18, the change is from monochromatic to frequently bicolored. On the east coast of the Barahona Peninsula, dewlap color changes from extensively red-orange at locality 29 to generally pale at locality 30. On the south coast of Haiti there is a striking but apparently gradual change from light or bicolored to uniformly grey from locality 38 to locality 40.

Differentiating Proteins. Of the twenty-five polypeptides examined in some or all samples of Anolis brevirostris, nine show substantial geographic variation. Six of these (LDH-1, IDH-1, IDH-2, αGpd-1, 6Pgd-1, and Est-1) were recognized previously (Webster and Burns, 1973). Transferrin (Trf-1), indophenol oxidase (Ipo-1), and Protein E (PtE) are of similar interest. The following comments qualify the results in Tables 00 to 00.

LDH-1. The important "a," "d," and "f" variants are quite distinct, with the reservation that an individual expressing both "d" and "f" might be difficult to recognize as such.

IDH-1. The "f" and "g" variants are well separated on the gel.

IDH-2 This is complicated by the frequent coincidence of its bands with the darker ones of IDH-1. The distinction between the "b" and "c" variants is questionable, and the frequencies of the "a" and "c" variants in populations dimorphic for IDH-1^g and IDH-1^f should be regarded as approximate.

αGpd-1. The "b" and "e" variants are quite distinct.

6Pgd-1. The "e" and "f" variants are well separated on the gel.

Est-1. Several of the distinctions involve small but apparently consistent differences in electrophoretic mobility. Such cases will be noted when their taxonomic implications are important.

Ipo-1. The "c" and "d" variants are so close than an individual expressing both might not be recognized as such.

PtE. The variants are distinct, but the data are not complete for a number of the earlier samples. Because very little intrapopulation variation was detected in unimportant geographic areas (as judged by other proteins), results from only a few individuals or from adjacent localities are used to fill the table.

Trf-1. This protein was observed in short series of plasma samples obtained from a minority of localities; otherwise the data are from whole animal homogenates and are of only satisfactory quality. Results from whole animal do not exclude the occurrence of any variant in low frequency in any sample.

Differentiation of Populations. The following associations of populations are apparent either from an inspection of the frequencies of the variants of the nine important proteins (Tables 00 to 00) or from consideration of the values of I based on 25 polypeptides (Table 00):

A. Sample 7' should be associated with samples 1, 2, and 3.[1]

B. Samples 39 and 40, from the south coast of Haiti, sample 46 from Ile de la Gonave, and samples 4 through 7 from north of Port-au-Prince should be grouped.[2]

C. All other samples appear to represent a geographically and genetically continuous unit, within which there is noteworthy geographic variation in protein variants.

Discussion

The samples examined in this study represent most of the distribution of A. brevirostris on Hispaniola. The three sets of populations recognized by protein phenotypes correspond to the informal sibling species A, B, and C of Webster and Burns (1973). Although the geographic area collected is much larger than in the earlier study, there is no evidence for additional siblings. While it is now possible to assign the name A. caudalis to Species B and to restrict A. brevirostris to Species C, leaving Species A undescribed, in this discussion A. brevirostris refers to all populations in this complex and the siblings retain the designations A, B, and C.

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[1] and [2] - see notes by Williams at end of section.

As in the previous study, the evidence on relationships was collected as a basis for inference about the significance of geographic variation in dewlap color. Since dewlap color may be important in the reproductive isolation of these parapatric siblings, the complications to the distributions of the siblings A and B require consideration. In particular, the occurrence of Species A at locality 7' appears to compromise the previous analysis of dewlap color variation along the Haitian coast north of Port-au-Prince. I suggest that this complication may be superficial and that population 7' represents a recent human introduction.

Like most of the localities, 7' is an isolated group of large trees that apparently is better habitat than the surrounding vegetation. The trees are a native mahogany, Swietenia mahogoni, planted along the road edge. On one side they are bounded by an extensive cane plantation, but on the other dry scrub provides acceptable A. brevirostris habitat and links the mahogany patch with other areas sampled. Recent introduction of Species A could have occurred with the seedling trees, through activity at the nearby complex of agricultural buildings, or simply because the trees border the main road from Port-au-Prince to the north.

Genetic evidence for the recent founding of this population is inconclusive but compatible with such an hypothesis. Population 7' appears to be fixed for an esterase variant that is common at localities 1 and 2 but which is almost absent from the nearest locality for Species A, locality 3. Genic variation is almost absent, but at localities 1, 2, and 3 (Table 00) it is moderately well-developed. New populations established by a few individuals often will have less variation than the parental population. This trend has been documented among anole populations established by human transport (Gorman et al., MS). While such suggestive arguments will never establish the history of population 7', I prefer to disregard it in the following discussion and as a cause for reconsideration of the analysis of Webster and Burns (1973).

The disjunct distribution of Species B is not surprising, as there have undoubtedly been historical changes in the extent and continuity of the arid forests of Hispaniola. The isolated records from the Tiburon Peninsula of Haiti, including recent collections from near Grand Boucan, indicate that A. brevirostris formerly occupied a large area now inhabited by A. distichus. A prior continuity of Species B, from the area north of Port-au-Prince to Jacmel and Marigot, could have included the entire coast of the Tiburon Peninsula or the low areas between its mountain ranges.

Esterase variants suggest that the Ile de Gonave population is more similar to those on the coast north of Port-au-Prince than to those at Marigot and Jacmel. Both present and inferred past distributions of Species B are suitable for colonization of Ile de la Gonave from Hispaniola. However, the set of characters diagnostic for Species B could have originated on Gonave, with subsequent invasion of the larger island.

Of the three siblings, Species C has both the most extensive distribution and the greatest geographic variation in protein variants. There are six diagnostic proteins in the comparison of sample 7 (Species B) and sample 8 (Species C), which is quite similar to others from Haiti's Plaine de Cul-de-Sac and adjacent areas in the Dominican Republic. However, the αGpd-1, Idh-1, and IDH-2 variants that characterize these populations are rare or absent in the vicinity of Cabral (samples 19-22). This transition seems to be clinal, but details are unavailable. The samples are both small and well separated. On the floor of the Valle de Neiba suitable road-edge vegetation is limited, and good habitat is often occupied by A. distichus ravitergum. Samples from the San Juan Valley and the eastern extreme of the A. brevirostris distribution share this increased similarity to Species B.

Populations of A. brevirostris between Barahona and Enriquillo are very distinctive. Their most striking characteristic is ecological; and, at least among sea level populations, they are unique. Most of the vegetation is mesic and seems more favorable to A. distichus, which is, however, absent. Instead, A. brevirostris is present abundantly, continuously, and even in deep shade. The dewlap is large and usually either strikingly bicolored or fully and richly pigmented, the body color is dark and more brown than grey, and even the habitus seems atypical. However, the protein data provide no indication of the major differentiation suspected on these criteria. This is true even for esterase, which in the A. brevirostris complex shows more intraspecific variation than the other proteins.

At Enriquillo there is a dramatic change in vegetation and geography, from mesic to arid and from the slopes of the Sierra de Baoruco to the plain that is the tip of the Barahona Peninsula. Anolis brevirostris changes also, and this is the one area where the transition is so abrupt that genetic differentiation of substantial biological importance could be expected. Although there are no diagnostic loci in the comparison of samples 29 and 30, the two regions do have different frequencies for variants of three proteins, Est-1, IDH-1, and IDH-2. All samples from the tip of the Barahona Peninsula are quite similar to one another and to the sample from Belle Anse.

On the south coast of Haiti, four proteins differentiate nearly all individuals of Species B from those of Species C. However, for three (Est-1, PtE, and Trf-1) there is a slight sharing of variants and for IDH-2 the data from Belle Anse do not exclude the presence of the Species B variant. These results suggest introgression, at least from Species B to Species C (all three loci) and possibly in return (Est-1). While the Species B variants are rare in the large sample from Belle Anse, they were detected nowhere else in Species C. Belle Anse is separated from the nearest sample of Species B (Marigot) by 29.5 kilometers of terrain that could be studied only with some difficulty. In this area, the Massif de la Selle rises abruptly from the Caribbean and A. brevirostris is apparently restricted to the vicinage of the coast. Its distribution is cut by two rivers that may be partial barriers to dispersal. The point of contact within this region and the extent of the suggested hybridization are completely unknown.

The two pairs of samples bracketing probable areas of contact between Species B and Species C represent two levels of detected genetic differentiation. There is evidence for introgression only in the case of the weaker divergence. However, the distance of the sampled localities from the area of contact may differ in the two cases. In addition, confidence intervals for estimates of genetic differentiation are relatively large when only 25 loci are considered (Nei and Roychoudhury, 1974).

Hybridization of A. brevirostris and A. distichus has been found at three localities, and at two of them it is quite common (Chapter XX). At each locality there is an apparent lack of introgression. Such mismating may occur in at least low frequency in many if not all areas of contact between distichoid species, including those of the A. brevirostris siblings B and C. The possible novelty of the contact on the Haitian south coast is introgression, which if real is associated with less observed genic differentiation than in other contacts of distichoid species (Table 00, Chapter XX).

Dewlap color variation for populations 1 to 7 and 8 to 12 appears to provide cues that could be effective in the reproductive isolation of Species A, B, and C (Webster and Burns, 1973). Not only do the siblings differ markedly from one another, but also from proximate populations of A. distichus. However, dewlap color variation elsewhere in the complex cannot be explained in the same terms. In the one additional area of contact between siblings, on the south coast of Haiti, there is no clear contrast. While the dewlaps at Jacmel are uniquely dark and those at Belle Anse are light and frequently bicolored, at Marigot they are intermediate. Around Jacmel populations of A. brevirostris are never far from those of A. distichus dominicensis, and the dark dewlap of the former may provide an adaptive contrast with the light one of the latter. While hybridization of Species B and C on the south coast is indicated by protein variants, introgression seems to be too limited to account readily for the pattern of dewlap color variation.

Dewlap color variation within Species C cannot be explained entirely by interactions with other distichoid species. Indeed, if dewlap color were under any form of directional selection, the extensive intrapopulation variation observed at several localities is unexpected. This failure of interspecific considerations to account for all intraspecific dewlap color variation is simply another example of the diversity that characterizes anoline biology.

It has been suggested that dewlap color is relatively unimportant within Species C, since this sibling seems to use the dewlap less than other distichoid species (Webster and Burns, 1973). This remains a plausible explanation, but I propose an alternative that is based on visibility and that is analogous to the work of Morton (1975) on bird calls. This suggestion makes extensive use of the comparative data and hypotheses of Rand (1974). For species in the complex faunas on large islands, Rand argues that predation discriminates against individuals who are needlessly conspicuous. Body colors tend to be nondescript to very cryptic. For facultative visibility, the dewlap is an important social signal.

While a primary function of dewlap use may be general advertisement, many of the social functions of this structure do not require that the individual attract attention indiscriminately. It is likely that the visibility of a displaying anole differs between deep shade and a sunlit perch. There could be considerable selection for a dewlap color that provides the optimum visibility. If it is adaptive to be very conspicuous during a display, then a striking dewlap would be expected. If it is adaptive to be cryptic under all conditions, then selection should favor a dewlap color that draws as little unsolicited attention as possible.

This is an explanatory rather than a predictive hypothesis. Without more substantial information on the functions of the dewlap and on the requirements for visibility over distance, there are no a priori grounds for suggesting which dewlap color should be associated with which habitat. Selection for optimum visibility is not exclusive to selection for interspecific contrasts, and observed dewlap color variation may seem inexplicable if both are operating. The following data on A. brevirostris seem to be congruent with the visibility hypothesis, but they are not a test of it.

All members of the A. brevirostris complex are quite cryptic (Fig. 0). While an experienced collector can develop an effective search image for these anoles, they are most readily seen in motion or in silhouette. By inference, visibility is an element in their selective environment. As noted previously, Species C seems to make relatively infrequent use of the dewlap. In filmed studies of captive Specie C males, Thomas Jenssen (personal communication) has confirmed this observation. This condition is presumably derivative and suggests that inconspicuous displays are adaptive.

The populations of A. brevirostris south of Barahona seem to be especially suited to a consideration of the visibility hypothesis. Although A. distichus occurs higher in the Sierra de Baoruco, congeners are absent from the coast. In these atypically mesic conditions, some A. brevirostris Species C have dewlaps that are almost entirely a rich orange brown. There is considerable variation, however, and E. E. Williams has observed that the darkest dewlaps occur in the most shaded habitats. Observations made in this study are comparable: the sample at locality 25 was taken from trees and fence posts bordering a pasture and locality 27 is relatively open vegetation near the beach, while both localities 26 and 28 are shaded ravines. Williams (1974) considers such a relationship between dewlap color and habitat to be common within the A. distichus species group. However, he suggests that the differences evolved to promote assortative mating maximizing local adaptation.

A rich orange brown dewlap color is characteristic of several races or species of anole that have a deep shade habitat. In contrast to other members of the Puerto Rican A. cristatellus species group, A. gundlachi almost never occurs in the sun. It has a dark orange-brown dewlap, while those of its close relatives are paler. One race of Jamaican A. lineatopus, ahenobarbus, has a dark orange brown dewlap. It occurs in shaded habitats on the mesic eastern end of the island. The two races occurring in open vegetation, A. l. lineatopus and A. l. merope, have lighter dewlaps.

Many forest species have other dewlap colors, and visibility certainly is not the only factor involved in determining dewlap color. The empirical association of dark, orange-brown dewlaps and shaded habitat was found in several independent comparisons, each involving the races of a single species or a set of closely related species. Each group of populations occurs on one of the Greater Antilles and occupies a range of habitats. E. E. Williams (1974) reports a relationship of orange or dark dewlaps and shaded dewlaps, not only in comparisons between races of two species but within races. At the least, this evidence argues that visibility deserves consideration in future work with anole dewlap colors.

Dewlap colors in Anolis brevirostris by locality. (Localities 1-12 are given in Webster and Burns (1973). Numbers in parentheses are sample sizes.

HAITI

Departement de l'Ouest

7' 2.2 mi NW Bon Repos: Dewlap skin entirely bright orange; dewlap scales pale yellow, giving the dewlap a sharp, pale margin.

DOMINICAN REPUBLIC

Independencia Province

13 0.5 km W Hato Nuevo: Monochromatic, dull grey orange or lighter pale orange, not in any case intensely pigmented (5).

14 24 km W Duverge: Monochromatic, pale yellow with a trace of orange (1).

15 On road to Puerto Escondido: Monochromatic, from light greyish yellow through dull orange to quite bright orange (4).

16 10 km W Duverge: Uniformly pale orange, with a very narrow pale yellow margin (1).

17 Balneario la Zurza, 5 km W Duverge: Monochromatic, dull orange, pale orange or bright orange (7).

Barahona Province

18 1.5 km S Las Salinas: Light pale orange or peach with a narrow pale yellow margin (2).

19 3.5 km W Cabral: Bicolored but approaching monochromatic, with pale yellow surrounding red-orange (2).

20 1 km W Cabral: Weakly to strongly bicolored, red-orange basal spot offset posteriorly, margin cream or pale yellow (5).

21 La Cueva on road to Polo: Bicolored, with an extensive and sometimes intense peach basal spot (8).

22 0.5 km E Cachon: Weakly to strikingly bicolored, sometimes nearly monochromatic; basal spot offset posteriorly, red-orange, modally covering half the dewlap; margin pale yellow (36).

23 Hotel Guarocuya, Barahona: Variable, from monochromatic to bicolored; spot peach to deep red brown, minute to covering most of dewlap; margin pale yellow (11).

24 13 km S Barahona: Slightly to strongly bicolored, spot orange-red or orange, somewhat offset posteriorly, margin light or pale yellow (8).

25 1 km S La Cienaga: Variable: dull to bright, monochromatic to bicolor. Margin usually cream, spot red-orange or orange and offset posteriorly (18).

26 9 km S La Cienaga: Red-orange except for a narrow margin of pale yellow (3).

27 S side Los Patos: Monochromatic red-orange or bicolored, the latter with the spot offset posteriorly and with a pale yellow margin (9).

28 1 km SW Los Blancos: Most of dewlap orange or red-orange with a narrow light yellow margin; often effectively monochromatic (5).

29 Canada la Chorrera, NW Enriquillo: Red-orange or orange over most of dewlap; light yellow margin sometimes somewhat wider anteriorly (8).

30 1 km NE Juancho: Most monochromatic, light yellow or cream to dull or bright orange, less frequently bicolored (16).

Pedernales Province

31 2 km W Oviedo: Mildly to strongly bicolored, with an orange or red-orange basal spot on a pale background (3).

32 1 km E La Pocita de la Mesa: Monochromatic light or lemon yellow (4).

33 La Pocita de la Mesa: Mildly bicolored, with an orange basal spot on a light yellow background, or less often monochromatic pale yellow (14).

34 1 km S Las Mercedes: Bicolored, with an orange basal spot (1).

35 3 km N on road to Las Mercedes: Bicolored, basal spot orange or pale orange (2).

36 4.5 km E. Pedernales: Very variable, from almost monochromatic pale yellow to strikingly bicolor, with a bright red-orange basal spot; modally a pale orange basal spot of modest size (18).

37 Pedernales: Nearly monochromatic to strongly bicolor; spot pale to intense orange bordered by pale yellow to light grey green (8).

HAITI

Departement de l'Ouest

38 Belle Anse: Nearly monochromatic to bicolor, with an orange spot on a cream background.

39 Marigot: Typically a uniform olive grey, but occasionally bicolor with an orange spot and a light margin.

40 Jacmel: Uniformly dark (or occasionally light) grey.

DOMINICAN REPUBLIC

San Juan Province

41 3 km W Sabana Alta: Variable, from pale with only a blush of warm pigment to light red-orange with a narrow pale margin; basal spot not sharply bounded (17).

Azua Province

42 N end of Los Corozos: Ground color usually very pale yellow; warm pigment (peach or salmon) almost absent to a poorly-defined basal spot; modal dewlap paler than at locality 41 (14).

43 2.5 km SW of turn to Padre Las Casas: Very variable, from almost entirely cream to having most of the dewlap richly pigmented; typically bicolor, with a peach or light red-orange spot and a pale yellow margin (14).

Peravia Province

44 2 km S San Jose de Ocoa: Cream to greyish with a trace of warm pigment.

45 La Gina, N of Bani: [pale, monochromatic] 1/

HAITI

Ile de la Gonave

46 Picme: Entirely cream to clearly bicolor, with an orange basal spot (4).

1/ Data inserted not available to Webster.

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Notes by Williams on "Variation in Anolis brevirostris."

1/ Locality 7' no longer exists. Haas and Williams saw the species A-like brevirostris and the line of mahogany trees in the summer of 1975. In the summer of 1976 the margins of the much improved north road were totally without trees in the same region. It was no longer possible to tell for certain where the line of trees had been. In one place there were some stumps burnt quite to the ground which may represent the former locality 7'.

Locality 7' initially worried Webster considerably, but his explanation (p. 4) in terms of human introduction of species A seems very probable. In any event, there can be no further investigation of the problem.

2/ The implication here is that populations 39 and 40 should be referred to Webster and Burns' species B. However, neither Williams nor Schwartz (in litt.) believe that the Jacmel brevirostris is B. Webster's opinion was based on electrophoretic similarity of classic mainland B, north of Port-au-Prince Gonave island brevirostris and the Jacmel population. But Webster also noted affinities (shared alleles) of the Jacmel population with the neighboring Belle Anse segment of species C and he also (p. 5) cites high similarity of eastern (Dominican)species C to species B. This does not seem a problem solvable immediately or directly on the electrophoretic evidence alone. Jacmel populations have a very different dewlap from B sensu stricto and are sympatric with distichus. Both mainland B and Gonave brevirostris exclude distichus. None of this is conclusive, and Webster is undoubtedly right in saying that the brevirostris complex once had a wider distribution. It seems better, however, to consider the relationship and status of the Jacmel brevirostris as clouded.

Hybridization of Hispaniolan lizards in the *Anolis distichus* species group

The three sibling species of the *A. brevirostris* complex have been informally termed Species A, B, and C (Webster and Burns, 1973). Further work (Williams, 1976) has established the present usage: *A. brevirostris* is restricted to Species C, *A. caudalis* is applied to Species B, and Species A lacks a formal designation. *Anolis distichus* is a complex of geographic races (Schwartz, 1968). Combined into the *A. distichus* species group, these taxa are well differentiated from all other *Anolis*.

Hybridization has previously been observed for only two pairs of West Indian *Anolis* species, although sympatric associations may in this lizard genus be complex and closely related species are frequently in parapatric contact. On Trinidad, the introduced populations of *A. aeneus* and *A. trinitatis* hybridize extensively (Gorman and Dessauer, 1966; Gorman, Licht, Dessauer, and Boos, 1971), but only a single hybrid individual is known for a natural complex fauna (Jenssen, 1977). *Anolis* species are highly visual and have well-developed repertoires of social behavior. It is generally assumed that females act on information presented in male displays to make reproductive decisions. Males of most species have a structure (the dewlap) that has a species characteristic combination of size, shape, and color and which is used [only] in social displays. For eight sympatric Hispaniolan species, dewlap color, pattern and size appear to provide a redundancy of information for species recognition (Rand and Williams, 1970). Accompanying the presentation of the dewlap is a pattern of body motions that can be complex and highly stereotyped (Carpenter, 1965; Ruibal, 1967; Jenssen, 1971). Body size and color may also provide species specific information (Williams and Rand, 1977). The rarity of instances of hybridization, even in situations of high species and population density, is explicable if some or all of these potential cues are consistently used for discrimination.

This paper reports hybridization between *A. distichus* and species of the *A. brevirostris* complex on Hispaniola. The implications of these observations for a previous inference about the significance of distichoid dewlap color difference (Webster and Burns, 1973) and for the general problem of reproductive isolation of *Anolis* species are discussed.

The observations

Both *Anolis distichus ravitergum* and *A. brevirostris* occur in the arid vegetation of the Valle de Neiba in the Dominican Republic. While one or the other occupies all but the bleakest habitats, the shape of the distribution of each appears to be intricate and the interface between them is consequently convoluted and of considerable length.

In August, 1970, T. and A. Schoener located a zone of contact in the middle of a pasture 2.5 km E of Cachon, Prov. de Barahona. Both species were abundant; individuals of each were observed together on a few trees, but the overlap of the distributions was slight. In October, 1973, I returned to this area to make observations and to collect. A second contact locality (0.5 km E of Cachon) was located on the opposite side of a small finger of the A. d. ravitergum distribution. On trees in this pasture A. brevirostris was abundant and A. d. ravitergum common. A number of individuals were morphologically intermediate, being lighter and larger than A. brevirostris but showing faintly the characteristic scapular spot and nuchal streak of that species. This locality was revisited several times to collect the parental species and the suspected hybrids. The 1970 locality was re-examined, and enough individuals were collected and released to establish the presence of the intermediate phenotype.1/

In the interior of the Valle de Neiba, 45 km to the west, hybrids were found at Balneario la Zurza (5 km WNW of Duverge, Prov. de Independencia). The road along the south side of the valley passes between a fossil coral reef and a large, shaded spring. Anolis brevirostris occurs in the drier, more open vegetation on and along the reef, while A. d. ravitergum is abundant in the large trees around the spring and in the agricultural area that it feeds. The two populations mingle narrowly along the road edge. Three females had color patterns that were intermediate between the two species and were similar to those of intermediate females collected 0.5 km E of Cachon.

Chromosome preparations were made from the testis tissue of 37 males collected 0.5 km E of Cachon (12 A. brevirostris, 19 hybrids, and 6 A. d. ravitergum) and of 6 A. d. ravitergum from 1.5 km E of Cachon. A standard air-dried smear technique followed by Giemsa staining was used. The male karyotype of A. distichus has been described and illustrated (Gorman and Atkins, 1969). That of A. d. ravitergum is identical. However, meiosis of hybrids is abnormal. Although testicular development is comparable to that in the parental species, chromosome pairing is highly disturbed and almost all cells at metaphase of the second meiotic division are diploid.

Twenty-five enzymatic and nonenzymatic proteins of individuals from both localities were examined with starch gel electrophoresis. Buffer systems and protein assays used are standard for vertebrates (e.g., Selander et al., 1971). Of 25 proteins examined, eight are diagnostic for this species pair (Table 1), with no observed sharing of variants. Hybrids are heterozygous for the eight loci corresponding to the diagnostic polypeptides. Field identification of individuals from 0.5 km E of Cachon was usually confirmed: two A. brevirostris and one A. d. ravitergum were confused with hybrids. As expected from the male karyology, there is no evidence for backcrossing, although hybrids are locally abundant. In the sample from Balneario la Zurza, five hybrids were identified by electrophoresis, including two males that had been classed as A. d. ravitergum.

1/ In this population of A. brevirostris there is a polymorphism for supernumerary chromosomes. Observed male diploid numbers range from 33 to 36. All A. brevirostris differ from A. d. ravitergum in the morphology of one pair of small macrochromosomes. Meiosis is abnormal in the hybrids.

Elsewhere on Hispaniola there are several known contacts of populations representing the A. brevirostris complex and A. distichus. At Montrouis, Haiti, both A. brevirostris Sibling A and A. distichus dominicensis are abundant. In an electrophoretic study of proteins of 82 A. brevirostris and 22 A. distichus, one "A. distichus" was an F_1 hybrid (Table 0). There is no evidence for backcrossing. 2/

Discussion

Hybrid morphology appears to differ between the two Valle de Neiba localities. At 0.5 km E Cachon, the hybrids are intermediate in coloration and most individuals were correctly identified on that basis. At Balneario la Zurza, female hybrids seemed more similar to A. d. ravitergum but were recognizably intermediate, while the two males were not suspected. Differentiation of A. brevirostris between the two localities may be responsible for the dissimilar results of hybridization. As summarized by Nei's normalized identity of genes, I (Nei, 1972), the electrophoretic data indicate that the two parental populations of A. d. ravitergum are almost identical, while the A. brevirostris have diverged considerably (Table 0). The Balneario la Zurza population of A. brevirostris is similar to those in the Cul de Sac Plain of Haiti (see Webster and Burns, 1973). The differentiation of the eastern populations is described in greater detail elsewhere (Webster, above).

In the Valle de Neiba, the dewlaps of male A. d. ravitergum and A. brevirostris are similar but not identical. Both are bicolored, with a pale margin surrounding a darker or brighter spot of variable size. In A. brevirostris the spot is offset somewhat toward the posterior margin of the dewlap, is red-orange, and ranges from almost absent to the entire dewlap except for a very narrow margin. The modal condition is a spot covering about half the area of the dewlap. In A. d. ravitergum the spot is centered, orange rather than red-orange, and on the average covers perhaps a third of the area of the dewlap. These differences are apparent after close inspection, but they are minimal in comparison to many of those observed between closely related Anolis species. It seems unlikely that they would provide effective cues for species recognition over much distance and in variable lighting.

At Balneario la Zurza, the dewlaps of A. d. ravitergum range from uniformly light yellow orange to strongly bicolored, with an orange basal spot. Dewlaps of A. brevirostris are all monochromatic and orange, but both the intensity and vividness of the color vary. While the more strongly bicolored dewlaps of A. d. ravitergum are distinct from those of A. brevirostris, dewlaps do not seem to consistently differentiate these populations.

Species of the A. distichus group often present contrasting dewlap colors in areas of contact or proximity. Such differences suggest that dewlap color is important for species identification and reproductive isolation (Webster and Burns, 1973). At the Valle de Neiba localities, the high frequency of hybridization in the absence of distinct dewlap colors supports that conclusion.

2/ See note by Williams at end of section

Although similar in dewlap color, A. brevirostris and A. d. ravitergum differ in both body size and color. Anolis brevirostris is smaller (Table 0) and has a complex, fine-grained pattern of greys, blacks, and whites. The scapular patch and nuchal streak are the most conspicuous markings, but not especially so. Anolis d. ravitergum is larger, and brown without any striking pattern. Both body size and color appear to be important in Anolis species identification, especially in simple (e.g., two-species) faunas (Williams and Rand, 1977.) If there is any discrimination at the Valle de Neiba localities, body size and color may be more important than the minimal difference in dewlap color. Display patterns have not been examined, but potentially they provide further information for discrimination.

While mismating is frequent, it may involve proportionately more females of one species than of the other. Directly or indirectly, size is important in the sexual success of lizards (Trivers, 1972), and it is possible that A. brevirostris females are often seduced by the large size of A. d. ravitergum males.

The hybrid between A. brevirostris sibling A and A. d. dominicensis represents an area where a strong difference in dewlap color (entirely orange and pale yellow, respectively) appears to favor reproductive isolation (Webster and Burns, 1973; Montrouis, Haiti, is locality 3). The incidence of hybridization is lower than in the contacts between A. brevirostris and A. d. ravitergum. Possible cues for species identification also include body color (light green for A. d. dominicensis) and body size (A. brevirostris sibling A is the largest member of the A. brevirostris complex and at this locality is larger than A. distichus: Table 0).

One or both of the parental species in the Valle de Neiba is mismating with considerable frequency. Since the hybrids seem to be invariably sterile and are viable and robust enough to compete with nonhybrid individuals, adaptations minimizing hybridization are expected. The existing situation can be attributed to relative recency of contact or explained by behavioral complications not yet considered.

Hybridization of A. aeneus and A. trinitatis occured after human introduction of both species to Trinidad (Gorman and Dessauer, 1966). The habitat preferences of A. lineatopus neckeri and A. grahami are quite distinct, and human disturbance of natural vegetation may have produced greater opportunities for hybridization. Both A. brevirostris and A. d. ravitergum are indigenous to Hispaniola. The arid vegetation in which they occur has been substantially affected by human activity, but it is more probable that such change has modified the distributions of these species rather than the extent to which they overlap. It is unlikely that A. brevirostris is a recent introduction to the Valle de Neiba. However, A. d. ravitergum may be a recent invader. It has a considerable distribution to the north and east of the Valle de Neiba (Schwartz, 1968), and until recently its range could have been bounded by the Rio Yaque del Sur. Definitive evidence for the antiquity of the zones of hybridization cannot be expected. However, in any further investigation of these species it will be important to search for hybridization

around the entire periphery of the A. d. ravitergum distribution (e.g., in the eastern end of the San Juan Valley, Prov. de Azua; and south of San Jose de Ocoa, Prov. de Peravia). There is no morphological evidence indicating greater potential isolation in those areas, but if such contacts are more ancient than those in the Valle de Neiba, less hybridization may be observed.

In this discussion of cues for species identification, appropriate and effective female choice has been assumed. If a proportion of matings occurs without female choice, a stable incidence of hybridization could be explained. For instance, "hypersexuality" is reported for male A. lineatopus neckeri, leading to the suspicion that a male of that species subdued a female A. grahami to produce the observed hybrid (Jenssen, 1977). I doubt that the high frequency of hybridization at the Valle de Neiba localities is due to such a breakdown in Anolis courtship, but rape can certainly explain the hybrid between A. brevirostris sibling A and A. d. dominicensis. Perhaps careful search will discover a low frequency of hybridization in other, perhaps all, contacts between distichoid species. The development of strong contrasts in dewlap color and other cues may reduce but not eliminate the frequency of mismating, since both male sexual aggression and female choice would be adaptive.

Acknowledgements.

I thank B. B. Simpson for assistance in the field and M. Thayer for assistance in the laboratory. NSF Grant GB-37731X to E. E. Williams supported this study.

Note by Williams on "hybridization"

2/ Brevirostris species A and distichus. It has been a matter of interest to Williams just what the ecological interrelations of species A are with distichus. He had in fact seen the sympatry of species A and distichus at the Artibonite River as far back as 1959, and it was his major reason for recognizing brevirostris as distinct from distichus. However, there have been no studies of the interactions of the two species. Accordingly, in addition to collecting samples for laboratory use, the summer 1976 crew in Haiti (Crews, Wu, Haas and Williams) checked the local distribution of the two species in a number of selected areas between Montrouis and Desdunes Bois. The survey suggested some tentative conclusions. A. distichus occurred in situations, often very local, that were relatively mesic,with some moisture and shade evident. In such situations it was often syntopic with species A, occurring on the same trees. In more uniformly open habitats species A, both in terms of observations and of specimens brought in by the local people, appeared to occur alone. However, none of the open areas visited north of Montrouis were as stark or arid as most of the range of species B to the south.

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The best memorial to Preston Webster will, of course, be the continuation of his work. Even while he was writing his thesis, numbers of us were peripherally involved, procuring specimens for him or giving him reports on the distichoids we encountered, sometimes casually as adjuncts of other studies, sometimes actively (Williams) as a matter of personal interest in certain of the problems.

There is in fact already at hand additional information on the distichoid anoles that is the result partly of the collateral work mentioned above and partly of work done in the summer of 1976. At the moment this additional information is best treated as footnotes or appendices to Webster's more fully organized data.

Additional notes on distichoids

by Ernest E. Williams

1. El Recodo Road

El Recodo Road was discovered as part of the search for the red dewlapped cybotoid that was described as Anolis marcanoi. It is a very accessible dirt road of good quality starting due north from the eastern edge of Bani just beside the police station. A left turn is made at the fork by a large store and there are then no problems other than two fords, the first possible in a rented car, the second not so.

The El Recodo Road provides a very interesting transect through three distichoid populations, from distichus into brevirostris and then into distichus again. (Curiously, marcanoi begins just before the first ford, a little before brevirostris, and continues beyond it, at least as far as the second ford.)

The road has been traversed no less than three times and collected twice. The last survey (by Barbara Wu, Patricia Haneline and Williams) involved no collecting, but crucial parts of the road were checked at .2 kilometer invervals censused by walking.

Just outside Bani at the beginning of the road, we are clearly in classic distichus ravitergum: the bodies grey or grey brown, sometimes with a green tinge, the dewlap pale yellow or with a very slight orange blush. A. distichus continues to the first ford, at 5.4 km N of the main road; locally in shadier, wetter areas the dewlap may have more orange, but in addition to this local variation, there is some clinal tendency to the increase and intensity of orange or red in the dewlap and green pigment in the body as the ford is approached. Even on the south side of the ford there is high variability: one specimen seen in a small, deeply shaded grove was descriptively close to ignigularis - a very green body and the dewlap more than half deep red orange. Another, although the body was quite green anteriorly and yellowish posteriorly, had a pale dewlap. Still others, again with green anteriorly and bronze posteriorly, had intermediate dewlaps.

Distichus continues north of the ford, but this is an open cultivated area with even the trees along the streem as it parallels the road not providing any heavy shade. The distichus are seen most often on fence posts. Dewlaps are yellow or with a faint blush. From the ford to 6.7 km from the main road there were seen in 1976 only distichus except for two widely separated brevirostris. From 6.7 to 7.5 brevirostris predominated with an occasional juvenile distichus. From 7.5 to 7.9 km from the main road there were only brevirostris. At 7.9 km there was again distichus and precisely at this point of overlap an interspecific mating was seen. North of this locality there was only distichus - greenish in body color but with pale dewlaps with orange blush in the dewlaps.

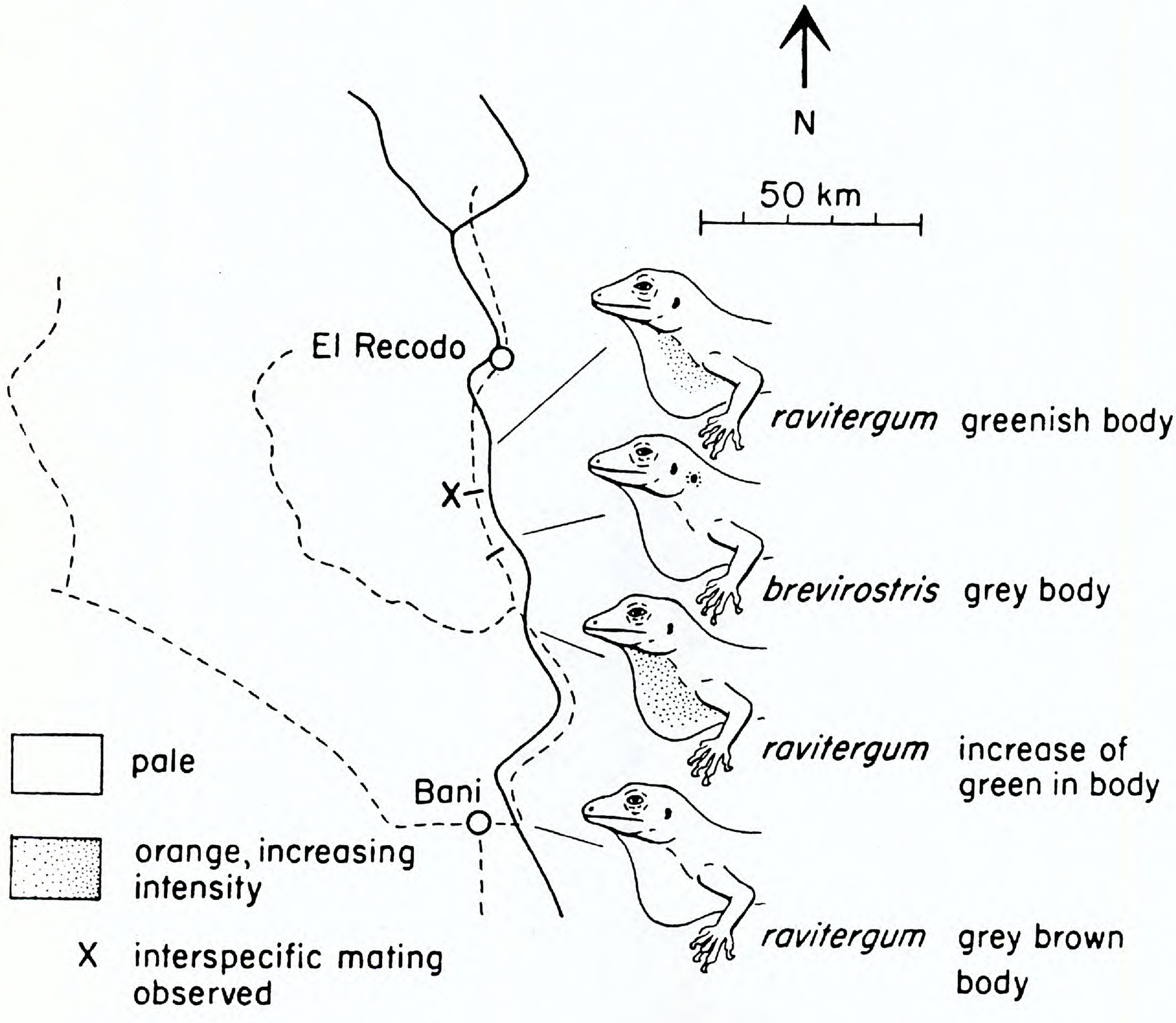

FIG. 1. El Recodo Road - broken line

(Ravitergum for any but the southernmost populations may not be a correct evaluation.)

This is an extraordinary situation. It is hard to know what to call the various populations of distichus. Genetically the populations south of the ford, indeed up to the narrow zone of brevirostris, would seem to be in contact with distichus ravitergum and perhaps only color variants of ravitergum. Intergradation with ignigularis seems implausible. These populations are remote from any mapped populations of that subspecies. Again north of the brevirostris zone the distichus are not readily allocatable. Descriptively they are very like dominicensis, but again they are remote from any mapped areas of dominicensis.

Another portion of the puzzle is that, while it is indeed different in body color, the brevirostris which intervenes between the two populations of distichus is minimally different in its uniform pale dewlap from the dewlaps yellow or with a faint blush of the intimately adjoining distichus. It is, in fact, clear from the observed interspecific mating that mating mistakes are being made.

No ecology peculiar to the brevirostris zone accounts for its presence. There are obviously several problems here crying for solution.

2. "Green Chapel Road"

A little distance outside the city of Barahona and just beyond the police post is a dirt road to the west at the beginning of which is a shrine which, in 1971 when the road was first explored, was painted green. This road has ever since been called by Williams and by Schwartz the "Green Chapel Road," although the shrine is not a chapel and it may be painted a different color in any given year.

This road seems nowhere to be properly mapped and it has forks and turns that have caused confusion. One of its multiple alternative routes leads eventually to a so-called "Haitian village" at which the strange montane anole, Chamelinorops wetmorei, is common.

At much lower elevations it provides a complication in the distichoid story which is of interest and was first discovered in 1971.

The early portions of the road are in scrub or along cultivated fields and only brevirostris is seen here. Eventually - after two left forks - a relatively shaded village in a ravine is reached and the road crosses a very shallow ford. Here, in the dark area by the ford, there are distichus with pale dewlaps, one with a distinct orange blush. Collections were made by Roughgarden, Williams, Huey and Webster. On the sunny hillside above the ford, Webster in 1971 found a brevirostris. A lizard market at the ford brought in brevirostris from sunny areas near the houses. Exploration by Jonathan Roughgarden and Williams up this same segment of road and over a considerable rise in elevation found at four stops distichus, all with pale dewlaps.

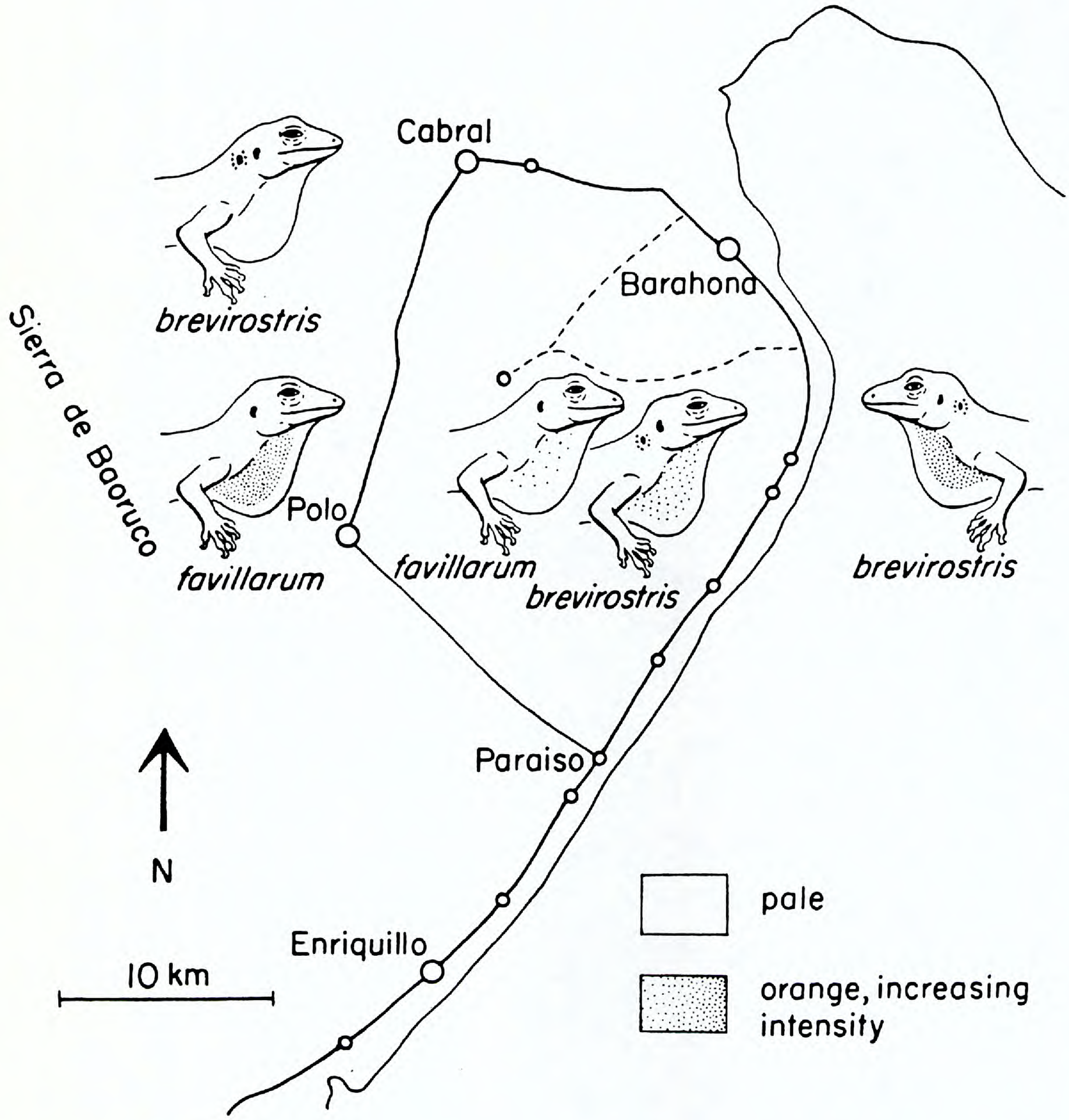

FIG. 2. "Green Chapel Road" - broken line
(Only the beginning of the road north of Barahona can be accurately mapped.)

The interest of this phenomenon comes from geography. The "Green Chapel Road" climbs the flanks of the Sierra de Baoruco from the east.

Another road enters this segment of the Sierra do Baoruco from the north, coming out of the town of Cabral, and leads to Polo. The arid woodlands on the lower parts of the road are occupied by brevirostris, but the high valley which this road enters is the type area for an orange-dewlapped race of distichus named favillarum by Schwartz.

On the upper slopes of the Sierra de Baoruco there cannot be many kilometers between the orange-dewlapped populations of distichus and those with pale dewlaps. When the latter were first discovered, they seemed so much like dominicensis that fantasies were proposed in which a tongue of dominicensis extended onto the southern slopes of the Sierra de Baoruco from, perhaps, Haiti.

These fantasies, however, were not to have a long life. Webster studied the pale dewlapped population from the ford electrophoretically and pronounced them identical in proteins to the classic orange-dewlapped populations called favillarum.

The "Green Chapel Road" was reinvestigated by Haas in the summer of 1976. He took a somewhat different route - a right fork at the first village - from that investigated by Roughgarden et al. in 1971. His account of both geography and animal distribution differs from that found by the 1971 party. However, the biological picture remains the same. In the early part of the road he found only brevirostris, somewhat variable in dewlap color but more often orange with a yellow border, but ranging to an orange blush and rarely yellow with no orange. At km 20 (11.5 km beyond his turn-off) he encountered a crossroad village, a ford, large trees with epiphytes and a ravine. One brevirostris and a small distichus were seen on fenceposts. At the edge of the ravine distichus were common (no brevirostris) with a very slight orange blush to the dewlap. The single brevirostris from the fencepost had a moderate blush to its dewlap.

At km 21.0 in a somewhat drier area, only distichus is seen - six on a large tree. The dewlaps have a pale orange blush.

At km 22.1 in a dry open area, five male brevirostris were seen, two on large trees, three on fenceposts, dewlaps with moderate orange or a blush.

At km 22.5, a coffee plantation, the animals are on trees in the shade. One is a brevirostris. Two male distichus caught had light yellow dewlaps with no trace of orange; two other distichus seen dewlapping are the same.

The complexities of this situation cannot be resolved without more information but on both the northern and the southeastern slopes of the Sierra de Baoruco some relationships remain consistent. The brevirostris in both cases are characteristic of the drier, more open, often lower areas. Distichus do not occur till moderately high elevations and consistently in

moister areas. The situation between the two species seems simpler on the north side, since, as it is currently known, distichus with orange dewlaps (favillarum) occupy a zone above brevirostris with pale dewlaps. There is no demonstrated contact nor interdigitation. To the southeast, the two species are known to occur together, but brevirostris is more frequent in dry situations, distichus in moist areas such as ravines, stream banks, and areas with larger trees. Just as ecologically the differences, while real, are not very sharp, the difference in dewlap color is again real, not as radical as between classic favillarum and Valle de Neiba brevirostris, but reversed in terms of depth of color. It is brevirostris that has more orange in the dewlap, distichus that is pale. The brevirostris of the southeastern slopes are continuous with populations still further south on the east coast of the Barahona peninsula that, as Webster reports above (localities 26-29), occur in quite mesic situations and have deep orange in the dewlap.

It is tempting to compare distichus on the Sierra de Baoruco with species B as portrayed by Webster and Burns. On Webster's electrophoretic evidence, the whole distichus population at the top of the Sierra de Baoruco is favillarum, variable, however, in dewlap color: orange where it adjoins pale brevirostris, pale where it adjoins more highly colored brevirostris.

On Haas's evidence, however, the intimacy of contact and the lack of sharpness in dewlap contrast in the "Green Chapel Road" populations might mean a fair frequency of mating error. It is reasonable to expect some hybrid individuals at this contact of distichus and brevirostris.

3. Are there sibling species in the distichus complex: a question remains in the north-south transect.

The main north road in the Dominican Republic - the Carretera Duarte - provides a very convenient transect of the contact between the two distichoid taxa, ignigularis and dominicensis, which, at least at the center of their ranges, are sharply distinct in body and dewlap color.

In similar fashion, the main west road from Santo Domingo passes from the area of ignigularis into that of ravitergum, the latter (again at the center of its range) even more sharply distinct from ignigularis than dominicensis.

In similar fashion also, roads transect the presumed boundaries between three taxa at the tip of the Tiburon peninsula of Haiti which are again very strongly distinct in color.

When Schwartz in 1968 first fully described this sort of geographic variation in Hispaniolan distichus, the issue arose for both Williams and Webster of the species or infraspecific nature of the taxa described as subspecies. In several cases Schwartz's evidence for intergradation was

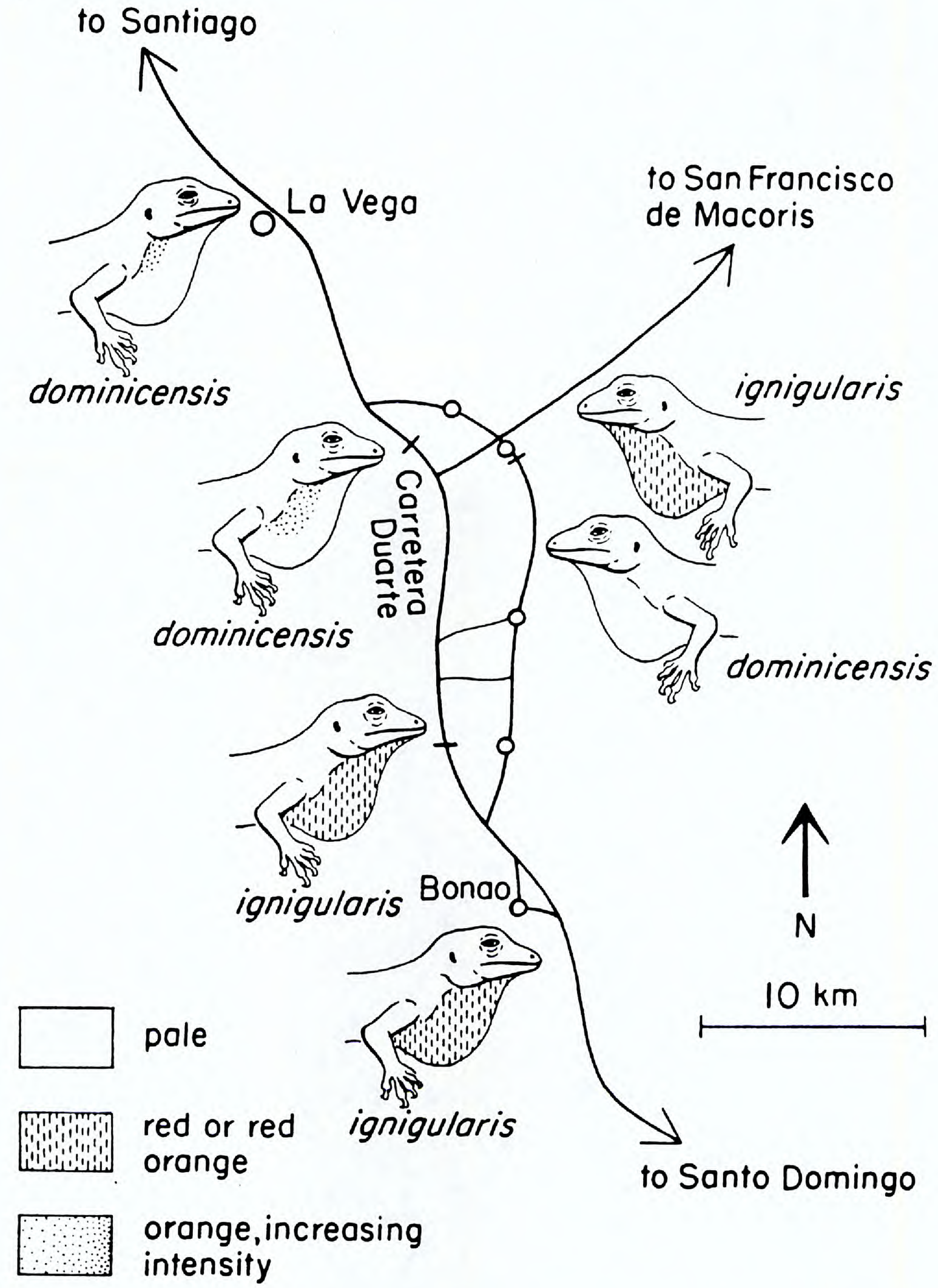

FIG. 3. The north-south transect

limited. Williams and Webster sought further field evidence on intergradation. The roads mentioned above made these studies quite feasible.

Webster was able to confirm both in the field and electrophoretically the genetic continuity of the three taxa at the end of the Tiburon peninsula. The ravitergum-ignigularis was more difficult. A great part of the presumptive intergrade area is in sugar cane and barren of anoles. However, both Webster and Williams checked various isolated local populations on the main road and north and south of it within the presumed intergrade zone. These did appear to show intergradation and again with certain of these Webster was able to show parallel intermediacy in electrophoretic characters.

Curiously the most accessible and most travelled transect has been less thoroughly investigated. Webster's attention was primarily directed toward Haiti and the Valle de Neiba and Barahona peninsula of the southwestern Dominican Republic. His samples of dominicensis were all from Haiti and he never made parallel collections of the extensive range of dominicensis in the Dominican Republic.

Williams and Roughgarden did census distichoids at intervals on the north road from Santo Domingo to Santiago and believed that they found evidence of intergradation. This was, however, before they were fully aware of the considerable variation in dewlap color within dominicensis far from any contact with ignigularis. No collections for electrophoresis were made and no study was ever done by Webster.

Webster was quite aware of this gap in our information but he did not regard it as a significant defect and continued to concentrate his attention to the west.

Williams, however, had become uneasy about the adequacy of the evidence on the relationship between dominicensis and ignigularis, and one of the objectives of the summer trip of 1976 was to redo the north-south transect with a view to pinpointing more precisely the area of intergradation. Barbara Wu, Patricia Haneline, Natasha Atkins and Williams therefore worked northward from Sto Domingo to find the point of change and then southward from Santiago, travelling backward and forward in the crucial area.

At Bonao, approximately half the distance to Santiago, the population appears to be classic ignigularis - dewlap more than half red with a narrow yellow rim. One of 10 specimens showed a slightly wider yellow rim.

Thirty-eight kilometers separate Bonao and La Vega. At the hotel on the main road outside La Vega a very variable population referable to dominicensis was seen. Dewlaps varied from a minimal basal blush to a small red spot with a very wide yellow border.

Two intermediate localities were examined. At 28 km S of La Vega (10 km N of Bonao) the individuals seen were ignigularis - dewlap red orange with a narrow border. At 12 km S of La Vega (26 km N Bonao) the animals were dominicensis - dewlaps with a peach or orangish blush.

Between these localities, along the main road, there were no favorable collecting sites for distichus; the area was too open.

There is, however, at this critical area a side road that essentially parallels the main road. This was therefore explored. At 7.5 km S of the northern junction with the main road and therefore within the area which should be critical, a small grove of big trees showed both individuals close in dewlap color to ignigularis and others as pale as dominicensis. At this place at least, there was no demonstration of intergradation.

An electrophoretic test of the situation is plainly necessary.

A digression. There are now a number of examples of narrow zones of contact between distinct populations in which electrophoresis detects interbreeding within the zone but no introgression on either side beyond the zone. Clearly this is better called hybridization than intergradation and each case should be investigated further genetically to the extent possible.

But such cases raise a question about zones of intergradation detected on museum specimens or even in the field. It will often not be easy and may be impossible to extrapolate from morphology to genetics. Problems of this sort may dismay the systematist but they are very real and must be confronted. Above all they are of prime evolutionary interest.

FORUM

The Editor provides here a space for discussion of the most challenging new discoveries and ideas. In the area of Anolis relationships, the most startling new development is the serious and important challenge to the previously fundamental concept of alpha and beta anoles.

The Editor has invited Shochat and Dessauer to put on record for readers of the Anolis Newsletter some of the unpublished evidence that seems to strike at the roots of the alpha-beta doctrine or dogma. The issue is certainly timely, since rather recently Savage has proposed the formal division of Anolis into two genera - Norops to be used for beta anoles, Anolis restricted to the alphas.

In a format which he hopes may be repeated in other issues of the Newsletter, the Editor has provided a comment on the Shochat and Dessauer thesis. The comment in this instance is somewhat skeptical. It is not intended to detract from the importance of the new evidence; the intent is cautionary. Much more work of the Shochat and Dessauer sort is obviously needed.

DAN SHOCHAT, in collaboration with Herbert C. Dessauer (Biochemistry Dept., Louisiana State University Medical Center, New Orleans, Louisiana 70112) has completed an immunological comparison of plasma albumins of 40 named forms of Anolis from the Caribbean Region. The major objectives of this study were to test current classifications of Anolis, and to apply protein structural evidence to the historical biogeography of the genus. Quantitative microcomplement fixation (MC'F) was the principal method used to estimate degrees of cross-reactivity in immunological reactions (Champion et al., 1974).

Immunological comparisons of the albumins are summarized in Table 1. Cross-reactivity is expressed as an Index of Dissimilarity (ID): the extent to which an antiserum concentration had to be raised for a particular albumin to give an MC'F reaction equal to that of the reaction with the homologous antigen. An empirical relationship exists between the logarithm of ID and the percent sequence differences (X) between proteins being compared: 100 log ID = 5 X (Prager and Wilson, 1971). 100 log ID is termed the number of immunological units (IU).

Animals from which albumins were taken are arranged largely according to the scheme of Etheridge (1960). Exceptions are noted in Table footnotes. Albumin affinities of anoles of the same species-series were estimated with reference antiserum from at least one member of the series. ID's obtained in such "within-series" titrations were below 1.5 with a few notable exceptions. ID's between albumins of Anolis from different species-series were obtained by cross-reactions involving antigens from members of one species-series and antisera against the albumin of a member of a different species-series. ID's obtained in such "inter-series" titrations exceeded 1.6 in all cases except those involving the acutus- and cristatellus-series.

The immunological evidence shows the Anolis albumins vary widely in structure. Using the empirical relationship between ID and sequence differences, we estimate that about 75 of approximately 580 total residues vary within each of the three widely divergent phyletic lines implied by our data. The probability is that a very large percentage of the primary structure of albumin contributes to determining the immunological differences found.

Taxonomic Implications

This matrix of immunological evidence furnishes an independent means for evaluating aspects of the evolutionary biology of Caribbean Anolis. The following is a summary of preliminary conclusions based upon these findings:

The albumin data are generally in close agreement with presently recognized species-series; of those tested only A. cybotes, A. valencienni and anoles of the acutus series seem to be improperly assigned. Anolis cybotes is distinct from all species tested; and, A. valencienni clearly belongs with the grahami-series. Members of the acutus-series, proposed by Gorman and Atkins (1969), seem best assigned to the cristatellus-series.

The magnitude of albumin divergence within species-series correlated well with current assessments based on more traditional criteria. The correlation was especially good for the latifrons-series for which we were able to test organisms widely different in taxonomic affinities. The MC'F data showed that there is little divergence in the other series tested.

Albumin affinities between different species-series are illustrated in Figure 1. Distance vectors, depicting magnitude of the divergence of taxa, are weighed averages of ID's expressed in immunological units.

The topmost triangle of Figure 1 illustrates affinities of the cristatellus-, bimaculatus- and grahami-series, which will be designated as the Central-Caribbean-Series-Complex (CCSC). The evidence is based upon inter-series titrations using antisera to albumins of A. bimaculatus, A. evermanni, A. cristatellus and A. valencienni. These results suggest that anoles of the three series have attained equivalent stages of divergence, with species of the cristatellus- and grahami-series showing somewhat closer affinities to each other than to species of the bimaculatus-series.

The bottom triangle of Figure 1 illustrates affinities of the carolinensis- and latifrons-series and the Central-Caribbean-Series-Complex. The highest ID's were obtained in cross-reactions involving antisera and antigens from these groups. Immunological distances between individual series of the CCSC and the latifrons- and carolinensis-series were of the same order of magnitude. To simplify the figure, these values were averaged so that vectors relate the CCSC as a group to the two other species-series.

The relative affinities of Anolis depicted in Figure 1 agree with a number of current hypotheses based on zoogeographic, morphological and karyological data, for example: (1) that the carolinensis- and latifrons-series are widely divergent from each other and from species-series of the CCSC; and (2) that the cristatellus- and bimaculatus-series have close affinities. The MC'F evidence gives a quantitative aspect to such estimates.

The protein evidence, however, is in conflict with the division of the genus into ALPHA- and BETA-Sections. The grahami-series and A. lineatus of the chrysolepis-series are classified as BETA anoles, yet they have closer affinities to the cristatellus-series of the ALPHA-Section than to species of other series of the BETA-Section (Table 1). Additionally, BETA anoles from other species-series are nearly as close immunologically to the grahami-series as the latter is to ALPHA anoles of the bimaculatus-series, A. cuvieri and A. equestris (Table 1).

Etheridge (1960, p. 131) proposed his ALPHA- and BETA-Sections with somewhat less than complete confidence: "It is not impossible that the transverse processes of the caudal vertebrae have been independently lost in several evolutionary lines of Anolis, in which case the various species-series of the section defined by the specialized sequence must be considered polyphyletic." Gorman (1965) interpreted karyological data as supporting the

ALPHA and BETA divisions, and later explained similarities in chromosomes of BETA anoles and ALPHA anoles of the acutus-series in terms of convergence (Gorman and Atkins, 1969). A simpler explanation is that this finding supports the immunological evidence for close affinities of these organisms.

Hypotheses Concerning the Phylogeny of Anolis

The following are preliminary speculations on phylogenetic aspects of the evolutionary biology of Caribbean Anolis, based upon taxonomic affinities suggested in Figure 1, evidence from historical geology and zoogeography and a time framework utilizing the protein clock hypothesis (Wilson and Sarich, 1969). Anolis albumins, like those of many other vertebrate groups (Maxson and Wilson, 1975), seem to have evolved at a rate of approximately 1.7 IU/ million years. This estimate is based upon ID's obtained in a number of albumin cross-reactions involving other iguanids and a careful evaluation of paleontological evidence.

The pattern which emerges agrees closely with many details of Williams' (1969) analysis of the subject, but suggests a number of alternative possibilities and may give a time dimension for major events.

The anoline and iguanine line presumably diverged about the middle of the Eocene Period (IU=90); equivalent to about 53 x 10^6 years before present) from a center of radiation in South America. During a mid-Oligocene radiation (IU=57; about 33 x 10^6 YBP), a number of distinct phyletic lines of anoline lizards originated. These included a "northern-phyletic-line" which led to the carolinensis-series, a "central-phyletic-line" which led to the CCSC, and a "southern-phyletic-line" which led to the latifrons-series.

Presumably, the "southern-line" spread across northern South America onto islands of its continental shelf, and northward onto the southern Lesser Antilles. Early radiations within this line probably occurred during the early Miocene. Protein clock considerations indicate that A. agassizi and A. luciae have been separated for about 20 million years from A. extremus and other anoles of the Lesser Antilles.

Progenitors of the "northern" and "central-lines" became established on Cuba and on the Puerto Rican bank, respectively. Perhaps one or both lines followed a route along the Nicaraguan Rise or established beachheads after transoceanic voyages. Cuba and the Puerto Rican bank have been consistent features of the Caribbean since the Eocene; and, the Nicaraguan Rise underwent an emergence from the late Oligocene to the early Miocene (Arden, 1969). An early Miocene radiation (IU=39; 23 x 10^6 YBP) of the "central-line" led to the bimaculatus-series of the northern Lesser Antilles and to the cristatellus-series of the Puerto Rican bank. The phyletic line which resulted in the grahami-series presumably diverged from a common ancestor with the cristatellus-series in the late Miocene (IU-28; about 16 x 10^6 YBP).

As these and other phyletic lines of Anolis spread across the Caribbean Region, speciation and extinction probably were common occurrences. Albumins of most species within the series studied were distinguished from each other by ID's of less than 1.5, suggesting that they had diverged from common ancestors since the mid-Pliocene.

Does the large proportion of relatively recent species suggest that most forms of previous radiations have become extinct, or were pre-Pliocene radiations far less productive in variety of forms? Are Anolis of uncertain affinities rare survivors of still other ancient phyletic lines? These and many other questions are posed by this new evidence.

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Table 1. Indices of Dissimilarity of Anolis Albumins.

Antigen Source	ID's with Different Antisera[a] CAR	EXT	BIM	EVE	CRI	VAL
			ALPHA-SECTION[b]			
Carolinensis-Series						
A. carolinensis	1.00	4.3	3.5	3.7	4.0	3.5
Latifrons-Series						
A. extremus	3.6	1.00	3.6	3.5	3.1	3.5
A. roquet		1.05	3.4		3.1	3.7
A. aeneus	3.9	1.23	3.6	3.7	3.6	3.5
A. trinitatis	3.7	1.26	3.4			3.7
A. richardi	3.3	1.32	3.6		2.8	3.5
A. griseus		1.38	3.6		3.1	3.4
A. bonairensis	3.4	1.8	3.4	3.8	3.3	3.0
A. luciae		2.3	3.4		3.1	
A. agassizi		2.5	3.8	3.4	3.7	
Uncertain-affinities						
A. occultus	2.7	3.2	3.7	3.1	4.4	2.7
A. cuvieri	3.2	3.4	3.0	2.8	4.0	2.4
A. equestris	3.6	3.1	3.5	3.0		2.6
Bimaculatus-Series						
A. bimaculatus	3.6	3.9	1.00	2.2	2.6	2.7
A. ferreus	3.4	3.9	1.27	2.2	2.2	2.5
A. leachi	3.6	3.1	1.25	1.9	2.3	2.3
A. oculatus	3.6	3.9	1.30	2.3	2.1	2.6
A. wattsi	2.9	3.5	1.29	2.0	1.9	2.5
A. marmoratus	3.4	3.9	1.31	2.3	2.1	2.7
Acutus-Series[c]						
A. evermanni	3.8	4.0	2.1	1.00	1.4	1.84
A. acutus	4.0	4.0	2.1	1.35	1.4	1.56
A. stratulus	4.3	4.2	2.4	1.39	1.55	1.89
A. distichus	3.7	2.9	2.0	1.50		1.77
Cristatellus-Series						
A. cristatellus	4.2	3.5	2.6	1.38	1.00	1.86
A. krugi	4.1		2.3	1.42	1.31	1.64
A. gundlachi	3.8	3.0	2.4	1.44	1.33	1.69
A. poncensis	3.9	3.9	2.6	1.37	1.33	1.84
A. cooki	3.8		2.2	1.25	1.35	1.76
A. scriptus	4.1	3.3	2.5	1.35	1.36	1.78
A. pulchellus	4.1	2.9	2.3	1.34	1.38	1.64
A. cybotes	4.6	4.2	3.2	2.8	3.5	3.3

Table 1. Indices of Dissimilarity of Anolis Albumins. Continued

	BETA-SECTION[b]					
	CAR	EXT	BIM	EVE	CRI	VAL
Grahami-Series						
A. valencienni[d]	3.9	3.6	2.7	1.87	2.2	1.00
A. reconditus		3.1				1.2
A. lineatopus	4.0	3.0	2.7	1.82		1.27
A. grahami	4.7	3.1	2.7	1.92	2.6	1.31
A. garmani	4.6	3.1		2.0		1.36
A. opalinus		3.6		1.99		1.38
Chrysolepis-Series						
A. chrysolepis	4.0	3.8	3.6	3.0		2.6
A. lineatus	3.2	3.2	3.0	2.1	2.4	1.65
Sagrei-Series						
A. sagrei	3.8	3.3	3.5	4.2	2.3	

[a]Antiserum to albumin of: CAR=A. carolinensis; EXT=A. extremus; BIM=A. bimaculatus; EVE=A. evermanni; CRI=A. cristatellus; VAL=A. valencienni.

[b]Classification according to Etheridge (1960), with exceptions noted below.

[c]Gorman and Atkins (1969) removed these forms from the Bimaculatus-Series and placed them in a new taxon of equal level based on karyotypes and protein phenotypes.

[d]Placed in this Series on the basis of the immunological data.

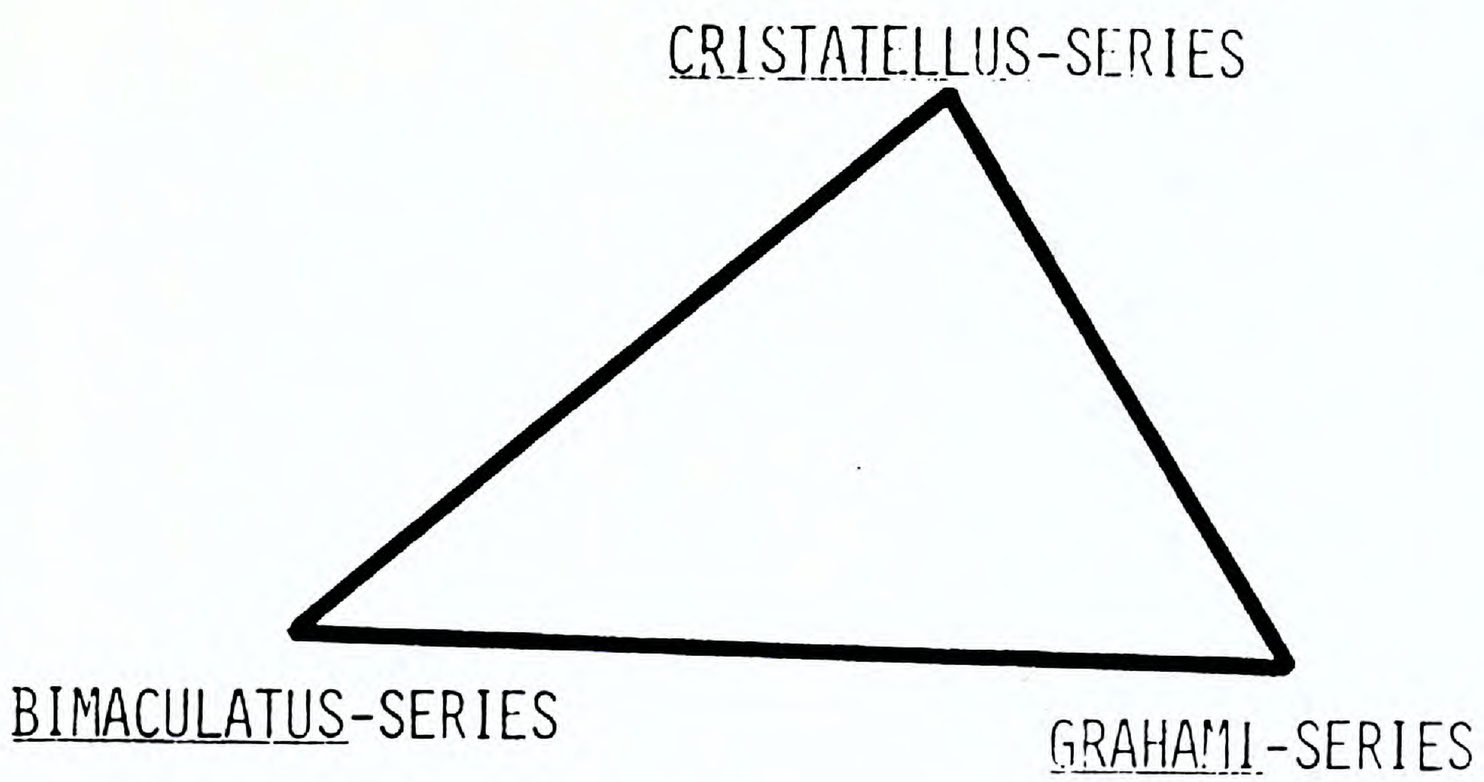


Figure 1. Affinities of species-series of Caribbean Anolis based upon albumin divergence. Top triangle illustrates affinities of series of the Central-Caribbean-Series Complex; bottom triangle illustrates affinities of the latter and the Latifrons- and Carolinensis-Series, Scale; 1 mm = 1 immunological unit.

FIG. 1

Comments on the Shochat and Dessauer Report

by Ernest E. Williams

The data of Shochat and Dessauer have to be accepted as valid. Their work has been careful and thorough. The meaning of the data is another issue, and other interpretations may be possible.

When any system of classification is in dispute, and a new scheme is proposed, any thoughtful response must look at two kinds of questions: 1. What does the new scheme explain that the old one did not, and 2. what rearrangements of species and of putative relationships do the new data and new scheme compel.

It may best set the background for these questions to place the controversy in a historical perspective. The Etheridgean classification has not been a carelessly accepted dogma.

A history of the analysis of West Indian Anolis

Before the Etheridgean analysis of the genus Anolis, nothing had been done but describe species. Occasional remarks were made about the affinity of species, but these were casual, subjective and ill-documented, and, when looked at from the point of view of later knowledge, frequently erroneous.

Before Etheridge, and this was, of course, the stimulus to his courageous attempt to analyze the genus, a number of people were attempting to make sense of a genus that was felt to be amorphous and too large. I, myself, just before Etheridge wrote his thesis, was attempting to make sense of West Indian anoles, and I was doing it in the conventional way by attempting to relate West Indian forms to specific mainland species (somewhat as has now been done for West Indian and mainland species of hylids [Trueb and Tyler, 1974]), but none of my efforts in this regard were convincing, and I viewed the problem with considerable unhappiness.

When Etheridge proposed his scheme, I did not at once believe him. I interposed objections (which I have now forgotten) and I sent him material to X-ray and sort out by his new technique, including unknowns and species I believed to be synonyms. Since he was dealing with a huge genus the systematics of which was primitive at best and in which it was unlikely that he would recognize unlocalized specimens, I was favorably impressed by his ability, on the basis of X-rays, to put animals in what I believed on other grounds to be the correct slot.

The major character on which Etheridge divided Anolis was not one which I or any systematist would automatically think of as significant at high taxonomic level: the presence or absence of transverse processes on caudal vertebrae. However, any systematist knows that the importance of a taxonomic character is something found empirically; it is not possible to judge the taxonomic worth of any feature on mere inspection.

Etheridge himself has emphasized to me (in litt.) that while working on his thesis he digressed from his survey of the place of anoles within the Iguanidae to check caudal processes in all families of lizards. It was only when he found the presence, or absence, or condition of the transverse processes typically constant in other families of lizards that he was willing to accord the transverse processes high taxonomic value in iguanids, including the anoles. For my part, it was this fact of usual constancy within lizard families plus the peculiar geographic distribution of this character within anoles that impressed me with its taxonomic relevance:

Thus Mexico and Central America down to Costa Rica had only anoles with transverse processes (betas) and the few anoles without transverse processes (alphas) in southern Central America had clear South American affinities and were easily interpreted as late invaders from there. The mixture all over South America of betas and alphas was explainable in similar simple fashion: the betas were northern invaders. Many were clearly representatives of species or species groups in Central America even up to Mexico. On the other hand, the alphas of South America in their diversity and in the distinctness of many of the species had the look of a relict endemic group.

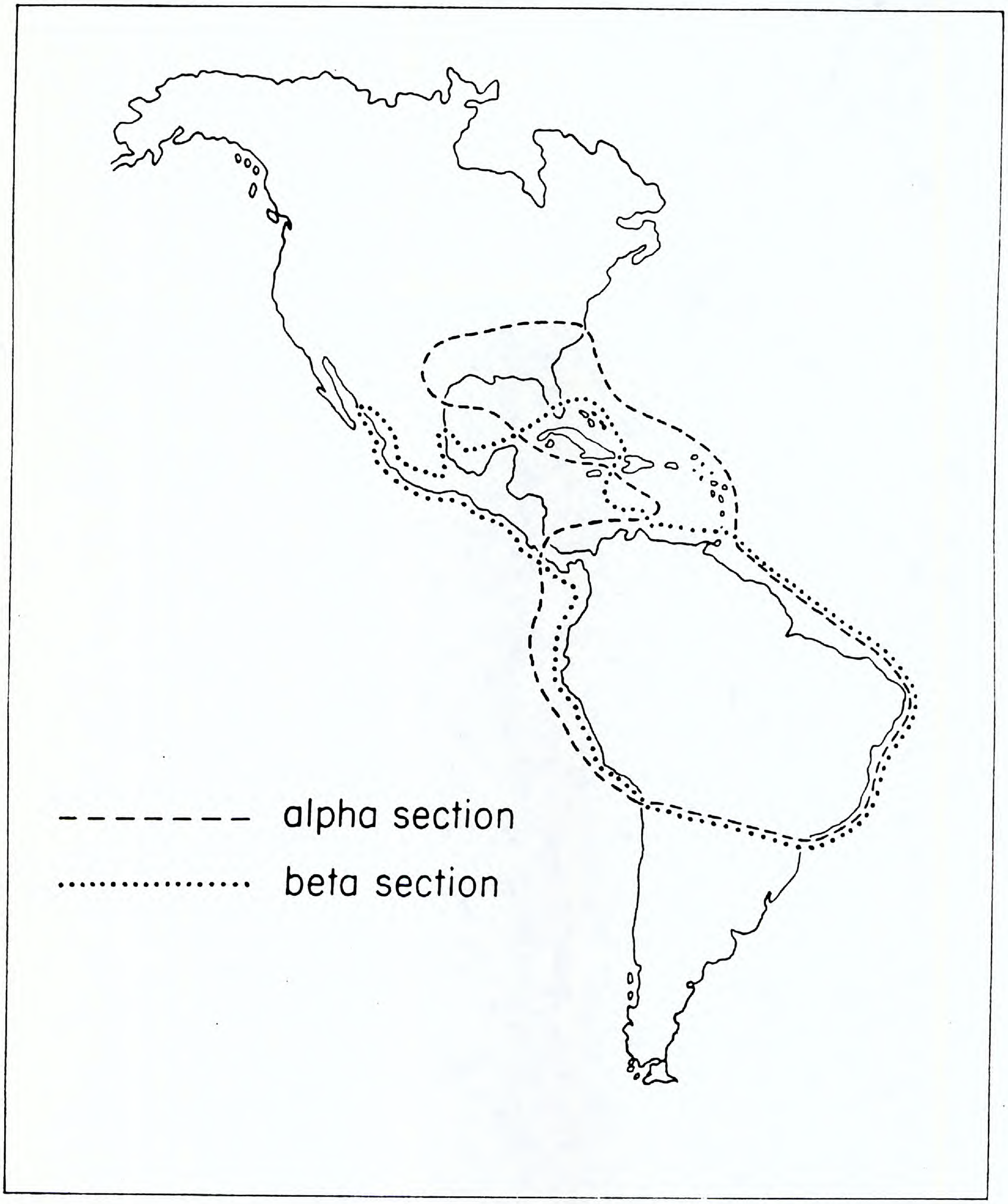
In the Antilles the southern Lesser Antilles had alphas which on multiple characters showed affinity with the South American alphas and were not (despite external appearances) very close to the species of the northern Lesser Antilles. Direct invasion of the southern Lesser Antilles from South America seemed very plausible.

In the Greater Antilles the eastern islands - Puerto Rico and Hispaniola - had only alphas; in the west Jamaica had only betas, Cuba had betas with affinities to Jamaica and alphas with evident relationships to Hispaniolan forms.

The northern Lesser Antilles again had alphas, in this case derived from Puerto Rican stocks. The southeastern United States had received its one alpha from Cuba. The Bahamas derived their fauna again from adjacent islands.

All in all, this was a tidy geographic picture with no anomalies or gaps in it, and the characters other than caudal transverse processes or lack of them seemed to support the neat picture of colonization always from adjacent sources.

[One emendation of Etheridge's maps of alpha-beta distribution must be made. Etheridge in his thesis (his map 2) erroneously restricted the range of alpha anoles to western and northern South America. This map has been republished by Savage (1966) (his fig. 12), and I have seen it referred to elsewhere. Actually Anolis punctatus, which he did examine, and Anolis nasofrontalis and A. pseudotigrinus, which Etheridge erroneously guessed to be betas (p. 165, his thesis), are alpha anoles extending to the coastal forest of Brasil, and in fact alpha and beta anoles are essentially coterminous in South America. That their distributions are not known to be exactly similar may be more a matter of inadequate collecting than of real absence from certain areas. Map 1 herein is therefore more nearly correct.]



MAP 1

One of the immediate virtues of Etheridge's system was that it released us from the futile search for separate mainland ancestors for each ecological type. It was not only on the alpha-beta dichotomy but necessarily on other characters as well that Etheridge declared most of the Jamaican anoles closely related - his grahami series - in a radiation which included several ecological types. For Jamaica no evidence since Etheridge's 1960 arrangement has significantly damaged his conclusions.

For me the Jamaican case was highly influential. I endeavored to see within-island radiations in each of the major islands. On Cuba, following Etheridge again, I saw separate radiations for alpha (carolinensis series) and beta (sagrei species group) anoles on that island and published figures (Williams, 1969) of the putative relationships. Again the currently available evidence seems to support the dichotomy on that island. For Hispaniola I have informally provided diagrams of possible radiations (notably for the 1972 Anolis Symposium) but I have never been confident enough to submit them to wider criticism by formal publication.

One thing, however, has always seemed clear; although there is no alpha-beta dichotomy on Hispaniola, the anoles there are not readily interpreted as the products of a single radiation. Some stocks seem clearly to have been invaders from Cuba, while the distichoid complex seems to have its ancestor near that of Puerto Rican stratulus. Etheridge and I have considered Anolis cybotes and its siblings to be relatives of the Puerto Rican cristatellus group. The ancestry of the cybotoids, however, may be in question (more about this below). The giant anoles of the ricordii complex are closest to A. roosevelti on Culebra in the eastern portion of the Puerto Rican bank, slightly less close to A. cuvieri of the Puerto Rican mainland.

However, by far the greater part of the Hispaniolan fauna belongs to a group that also includes A. carolinensis in the United States, all the alpha anoles of Cuba and A. occultus on Puerto Rico. This is a group probably autochthonous to Hispaniola and is there represented by a highly diverse radiation. It is defined by alpha tail vertebrae but a derived shoulder pattern is similar to or shared with the beta anoles.

There is here a degree of complexity that will not be adequately sorted out very soon.

In the case of Puerto Rico, on the contrary, I (Williams, 1972) have gone the whole way and interpreted all of the anole fauna as arising within the island bank, taking something a bit more primitive than the present day giants (A. roosevelti and A. cuvieri) as the ancestor of all the others and postulating that A. poncensis, the most highly derived form, is nonetheless a descendant of the first pre-giant invaders of the island. I endeavored to match a hypothetical ecological sequence of adaptations and a sequence of parallel morphological changes, all on the presumption that the Puerto Rican anole fauna was a single radiation occurring in place.

I do not even now think that the sequence of ecological changes is incorrect (the useful content of that paper may, in fact, be the concept of obligatory sequences in ecological adaptations) nor that I erroneously interpreted the primitive-derived ranking of the morphological changes. Neither of these, however, necessarily implies that there did occur a single intra-Puerto Rico radiation. The hypothesis, for example, that the fundamental division between pre-occultus and pre-giant stocks occurred on Puerto Rico has been shaken by the discovery of a species - A. sheplani Schwartz - much more primitive than occultus but clearly belonging to that lineage on Hispaniola. It now seems simplest to believe that the basic dichotomy between the occultus stock and the giant stock occurred on Hispaniola (or between Hispaniola and Puerto Rico), but, at all events, not on Puerto Rico.

Building on the Etheridgean framework, modifying and elaborating it as newer evidence seemed to require, I have recently erected a rather elaborate schema of classification of West Indian anoles (Williams, 1976) - using informal terms such as series, species groups and superspecies as well as formal nomenclature - and endeavoring, as Etheridge explicitly did not, to place every species in its correct place in a hierarchy.

The system has just now seemed complete and it is just now under fundamental attack.

Agreement and Disagreement

What are the agreements and disagreements of Shochat and Dessauer's data with the Etheridgean classification?

1. As Shochat and Dessauer have indicated, at the within-species group level there are more examples of confirmation than of disagreement. This is important. The immunological data confirm, for example, that the several Jamaican ecomorphs brought together as the grahami series do indeed belong together (they show an index of dissimilarity of 1.38 or less) and are a single radiation. Even the placement within the series of valencienni is a point in favor of Etheridgean phylogeny. Etheridge did not formally put valencienni in any group, although he considered that osteologically it belonged in the sagrei series. When, however, he made a dendrogram for the beta anoles, he showed the sagrei series as the direct derivative of the grahami series and showed (see Fig. 1) valencienni as an early and distinct offshoot of the sagrei stock. There is in fact no doubt that some characters of valencienni do point to membership in the sagrei series. Others point back to the ancestral grahami series and others are special to valencienni itself. Such a combination of characters is not unusual in early side twigs of derived groups.

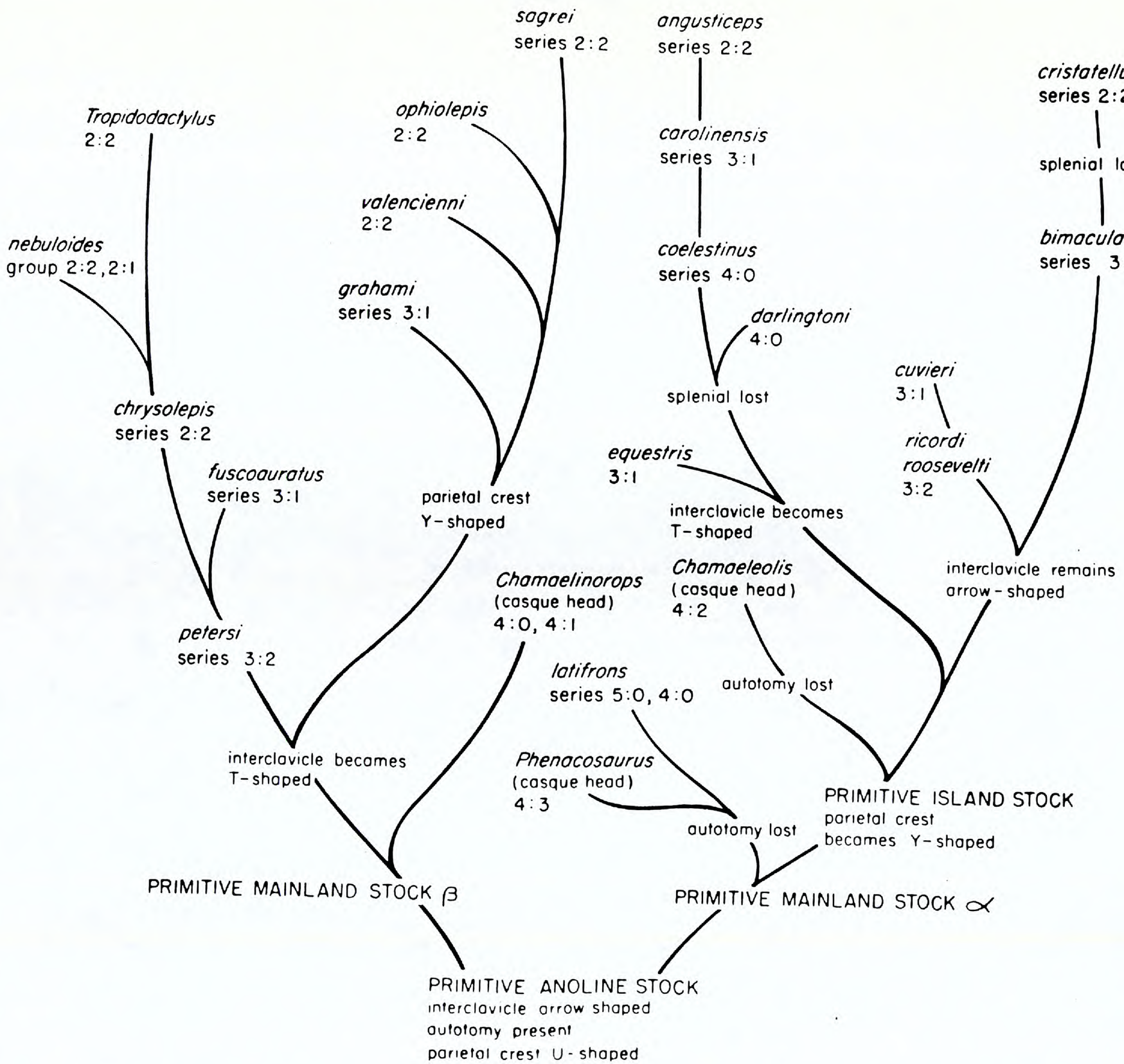


Fig. 1 (modified from Etheridge, 1960)

Similarly the common affinities of most of Etheridge's cristatellus series are supported by the new immunological data. Again different ecomorphs are placed together, and both the Puerto Rican trunk-ground anoles and the Puerto Rican grass anoles show an index of dissimilarity against cristatellus itself at the level of 1.38 or less. But as regards the Hispaniolan trunk-ground anoles, A. cybotes and relatives, there is disagreement: the index of dissimilarity against cristatellus rises to 3.5. On the basis of this result, Shochat and Dessauer reject the cybotoids as members of the cristatellus series.

This disagreement underlines an already existing controversy. Gorman has long advocated exclusion of cybotes from the cristatellus group on the evidence of karyotype and electrophoretic difference. I have maintained the Etheridgean viewpoint in spite of this counter evidence, and I shall attempt to show below that Etheridge's arguments for inclusion of the cybotoids in the cristatellus series still have considerable weight.

In the case of the bimaculatus series, Shochat and Dessauer again are partially in agreement, partially in disagreement with Etheridge's original grouping.

Gorman and Atkins (1969) have already divided Etheridge's bimaculatus series into a northern Lesser Antillean fraction and an acutus series which contained acutus of St. Croix and the Greater Antillean remainder of Etheridge's series - evermanni, stratulus and the distichoids. Shochat and Dessauer begin with this modified arrangement. They show that the restricted bimaculatus series again has within-group indices of dissimilarity in the 1.30s or below. The acutus series shows a somewhat greater spread: distichus tested against evermanni has an I.D. of 1.50. The interesting point, however, is that the acutus series gives an I.D. against cristatellus of only 1.4 to 1.55 while against the bimaculatus series where Etheridge put them the I.D.s rise to 2.0 to 2.4. Shochat and Dessauer on this evidence suggest merging the acutus and cristatellus series. In terms of the characters on which Etheridge erected group definitions, this is rather awkward, but from a phyletic viewpoint it is trivial: on any dendrogram the acutus series will have a partly divergent, partly intermediate position. It is because of this fact that Etheridge combined it with one of the two groups between which it lies, Gorman and Atkins made it a series of its own, and Shochat and Dessauer now suggest the third possible permutation. For each decision there has been good but different evidence.

Up to this point, in fact, there is no substantive disagreement between Etheridge's original scheme and the immunological data. It is in fact gratifying to have these intra-series relationships confirmed. The series Shochat and Dessauer have so nicely confirmed are the groupings that before Etheridge went unrecognized because we were searching for ancestors among mainland ecological equivalents.

2. In inter-series comparisons in contrast, the Shochat and Dessauer data appear to conflict without hope of rescue with the fundamental Etheridgean dichotomy between beta and alpha anoles. As Shochat and Dessauer say: "The grahami series and A. lineatus of the chrysolepis series are classified as beta anoles, yet they have closer affinities to the cristatellus series of the alpha section than to species of other series of the beta section."

In Table 1, I present the Shochat and Dessauer data in slightly modified form (averaged by series). I have placed the critical low I.D. values in a block within the table to make the comparisons more directly and immediately visible.

The data are not in question. There are, however, several considerations that make me question the first level conclusion that Shochat and Dessauer have drawn: that the beta and alpha sections are invalid.

(1) The immunological evidence is, as it stands, inadequate and hence unsatisfying. There are too many loose ends. I enumerate some of them.

(A) No phylogeny is provided. Shochat and Dessauer do give triangular diagrams of "affinities" first for the cristatellus, grahami and bimaculatus groups inter se and then for these three against the latifrons and carolinensis series. There is, however, no statement of phyletic relationship, only of degree of difference. On the immunological evidence alone, no doubt, they cannot do more; their data provide distance but not direction. However, the lack of information on ancestor-descendant or sister group relationships makes a new classification impossible.

(B) There is no satisfactory zoogeography. There is an attempt at this, but the evidence does not permit precision. This is not surprising since there are no data on Cuban anoles (although Cuba is suggested as a port of entry) or on Hispaniolan anoles (except for cybotes, which is left unplaced, although this huge island intervenes obtrusively between Jamaica and Puerto Rico.

(C) In fact too many anoles, examined and unexamined, are left in limbo. It is true that Etheridge hesitated about the placement of a number of species - A. cuvieri and A. equestris among them - but a new scheme would best demonstrate its superiority by showing definitively where they should go. No scheme can be satisfying that leaves these dangling. Again it is not especially useful to say that A. cybotes is not very similar to A. cristatellus. Certainly in chromosomes it is not. But the karyotype of cybotes is primitive, and this by itself cannot debar cybotes from ancestry to the cristatellus group. Does the immunological data say anything but that cybotes is older in its time of separation from the group than the species of the cristatellus group narrowly conceived are from each other? And if cybotes is not in the cristatellus group, where does it belong?

It may seem extraordinary to say that an immunological study that has dealt with 40 species is inadequate. This, however, seems to be the fact.

Table 1

Averaged IDs for Anolis series

	car	lat	bim	acu	cri	gra
car	1.0	4.3	3.5	3.7	4.0	3.5
lat	3.5	1.42	3.5	3.16	3.16	3.4
bim	3.4	3.7	1.24	2.15	2.2	2.55
acu	3.95	3.7	2.15	1.31	1.45	1.7
cri	4.0	3.32	2.4	1.36	1.29	1.74
gra	4.3	3.25	2.7	1.9	2.4	1.25
sag*		3.8	3.3	3.5	4.2	2.3
chr*	3.6	3.5	3.3	2.6	2.4	2.2

*Reciprocal tests were not done for the sagrei and chrysolepis series.

The diagonal averages within group IDs.

The problem appears more difficult and subtle than expected. Shochat and Dessauer cannot be blamed for using the material that was available, but however necessary logistically their choice of species has been, it has resulted in a biased sample. The carolinensis series, not lacking in numbers or diversity, is represented by two species - carolinensis itself and occultus. The latifrons series of Shochat and Dessauer is actually the roquet group of the southern Caribbean plus agassizi, an isolated and poorly understood species of a tiny Pacific island. The numerous mainland species of the latifrons group are not sampled at all. The sagrei group as examined contains only sagrei . It is unfortunate that the other members of the sagrei group are exclusively Cuban.

The mainland betas of Shochat and Dessauer are two species of one of Etheridge's three mainland series. None of the very many Mexican or Central American beta anoles are studied, and the two South American species which Shochat and Dessauer were able to work on seem not to be closely related to one another.

The immense virtue of Etheridge's analysis of Anolis was that - for the characters that it utilized - it was nearly complete. The X-ray technique that he used enabled him to obtain osteological information on most Anolis species, including even unique specimens.

Immunology has a vastly more laborious task without the same possibility of near total completeness. What Shochat and Dessauer have shown above all else is the necessity for much more immunological study.

3. Incomplete though the data may be for Anolis as a whole, the immunological data for one crucial case - the cross comparisons of the cristatellus and grahami series - seem inescapable. I have had the opportunity to examine Shochat's thesis, and it is clear that for this case there was abundant material carefully cross-checked and statistically analyzed. Whatever its meaning, there appears to be unequivocal demonstration that the albumins of the cristatellus and grahami series are much less dissimilar than the conventional placement of the two series had led us to expect.

Is there no other explanation? Does the protein clock always run at the same rate? On the latter point it seems to me permissible to be skeptical. Sarich, a very vigorous proponent of the clock hypothesis, has just recently said (Nature, January 1977): "....one can speak of an albumin clock and document that it generally keeps rather good time." This is not a strong statement, and it cannot afford to be. There are a number of instances now in which protein clocks are slower than expected. Sarich (1977) himself cites anomalously slow evolution of albumin in species of a genus (Dipodomys) and even slow classes (birds, Prager et al., 1974) have been mentioned elsewhere. Given knowledge that the protein clock does not always keep tood time, it is clear that each new case must be carefully calibrated.

It is unfortunate also that paleontological dates of origin for groups must be used to calibrate the protein clock. There is more controversy and uncertainty in paleontology than the proponents of protein clocks should be happy to acknowledge. Every paleontologist knows - and I speak as one who was at one time a paleontologist - that the acceptable level of uncertainty in this science is very high. Necessarily those arguments of proponents of a protein clock that rely on current paleontological evidence are their weakest.

But are there reasonable alternatives to the protein clock hypothesis for immunological data? Let us look at indices of dissimilarity or immunological distance as the naive systematist would look at any other similarity or difference. The naive systematist would first be unhappy with immunological distance as a single character.[1] Single characters, as the systematist knows, are frequently untrustworthy. The systematist is quite accustomed to anomalous single characters - the one primitive character that may persist in some taxon that is otherwise highly derived or the extraordinary specializations that are found in taxa that are in many regards quite primitive. "Primitive" as a statement for any character is only another way of saying that its evolution has been slow and specializations say only that evolution has been fast. This is a well known phenomenon as regards morphological characters. If we could treat protein evolution in the same way as that of morphological characters, we would have two different possibilities to suggest:

(1) Grahami-cristatellus albumins primitive, i.e. evolution slow as compared with that of other anoles. Similarity explained as retention of an ancestral condition.

(2) Grahami-cristatellus albumins advanced, i.e. evolution fast as compared with that of other anoles. Similarity explained by convergence.

It is my position that we do not at this time have the information on which to choose among the possible hypotheses to explain the relative similarity of grahami and cristatellus albumins: stochastic but regular, hence datable evolution; stochastic but slow, hence relatively limited evolution; fast convergent evolution, presumably driven by natural selection.

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4. The non-immunological evidence must itself be treated with more care and more attention to detail than has been customary. Etheridge's analysis - though I disagree with it at certain points - is distinctly more careful and more aware of alternatives than others have given him credit for. The defining character of alpha and beta anoles - the presence or absence of transverse processes on the posterior (autotomic) caudal vertebrae - has in most discussions - even by Etheridge - been treated too simplistically - more as a verbal formula than as a correctly observed anatomical feature.

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[1] Although several to many amino acids have changed, the total change is the character that we must deal with. Change of one to several amino acids is equivalent to the several stages of change of one morphological character.

Actually the transverse processes of the posterior caudal vertebrae of beta anoles are unlike those in any other lizards, so much so that Etheridge at one time considered the possibility that they were neomorphs - "pseudodiapophyses."

I think, in fact, that Etheridge has never sufficiently insisted on the uniqueness and uniformity of the diagnostic beta transverse processes. Fig. 2 here repeats Fig. 2 of the section on macrosystematics of the anoles (pp. 122-131 above) and demonstrates that the resemblance between the transverse processes of Chamaelinorops and of beta anoles is more imaginary than real. The only approach is seen in the rudimentary transverse processes which Etheridge discovered in some members of his cristatellus series and of which he says, "In this respect the [caudal] vertebrae are somewhat intermediate" between alpha and beta types. This intermediacy, as Fig. 2 shows, is real. But it is a fact not very convenient for the Shochat and Dessauer hypothesis of the close relationship of the cristatellus series to beta anoles that the rudimentary transverse processes occur in cybotes as well as cristatellus and scriptus (but not in other members of the cristatellus series). (The functional meaning of none of these caudal structures is known.)

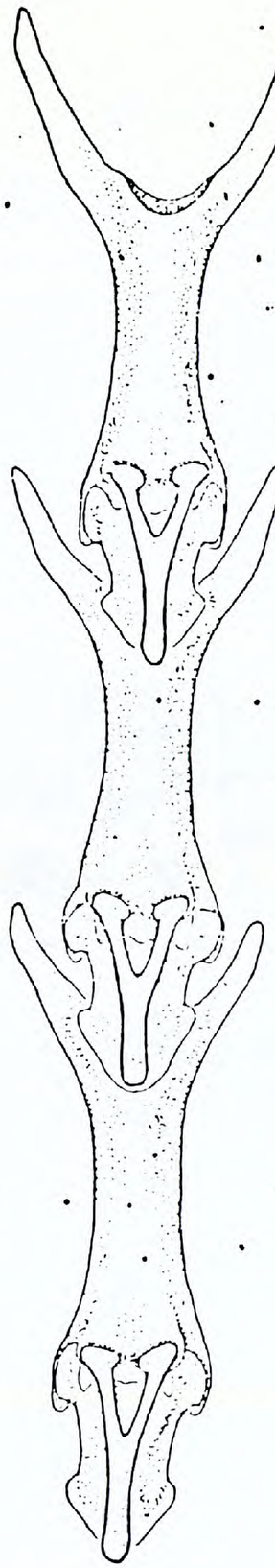
In any event, it is clearly a matter of considerable importance whether caudal transverse processes in anoles are a retention of a primitive character or neomorphs. If they are neomorphs, a wholly different history is implied from that in which beta transverse processes are primitive.

There is much about the beta anoles that is unprimitive, as Etheridge has emphasized. One such feature characteristic of all betas, but not unique to them, is the advanced type of shoulder girdle with T-shaped interclavicle. This elsewhere occurs only in the carolinensis subsection of the alpha series.

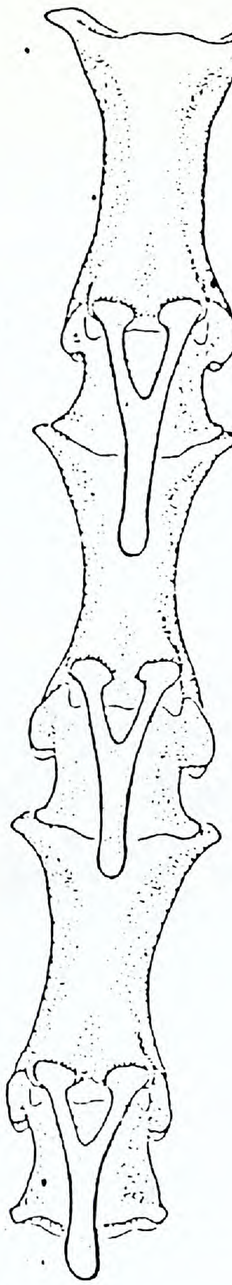
If all the beta anoles have unique neomorph transverse processes on the autotomic vertebrae and a highly derived shoulder girdle, it is evidently much more difficult to suggest that betas are not a natural group or that they have been derived from the cristatellus group which lacks both features. In fact, in considering these two characters only it would seem easiest to derive beta anoles from the carolinensis series, primitive members of which are resident in Hispaniola and in Cuba.

Etheridge explicitly considers this possibility on p. 194 of his thesis and expressly rejects it: "The major objection to this idea is not the unlikelihood of the evolution of pseudodiapophyses but rather the necessity for deriving all the mainland species of the Beta Section from some Antillean ancestor."

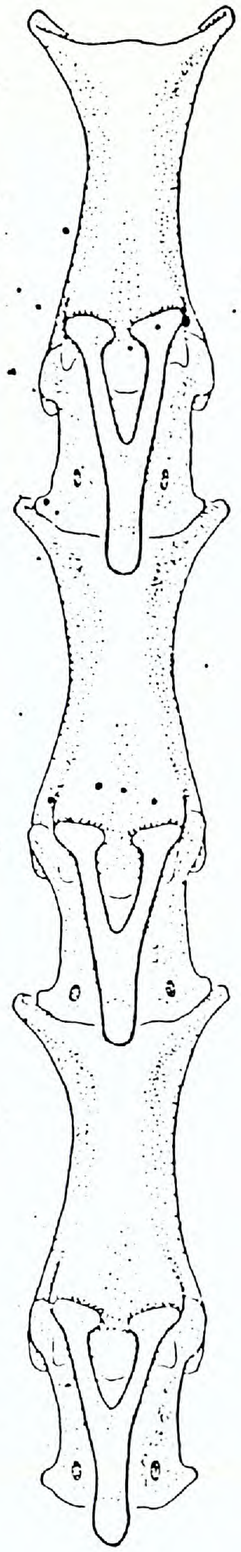
Shochat and Dessauer would also be unable to support this hypothesis. Their two species of the carolinensis series sampled are, by chance, carolinensis itself, one of the most derived members of the series, and Puerto Rican occultus, which, until the recent discovery of sheplani, was considered the most primitive member. Neither show a close relationship (Table 2) to evermanni, cristatellus or valencienni (although on these data occultus is as close to valencienni as to carolinensis).



A



B



C

D

FIG. 2. Anoline caudal vertebrae.

A. Anolis valencienni

B. A. cristatellus

C. A. cybotes

D. Chamaelinorops

Williams' current views on the relationship of anoles are given in fig. 5, p. 129.

But I do not raise the issue of the possible Antillean origin of the betas from the carolinensis group as a straw man to be knocked down, but only to show that there are many difficulties and possibilities to be assessed. Etheridge's own statement seems pertinent: "Various alternative phylogenies may be proposed to eliminate in part those difficulties which arise from the interpretation already presented. Each of these, however, begets its own difficulties, and they appear to be more serious than those of the original hypothesis."

I return now to the two questions with which I began: (1) What does the new evidence explain that the old Etheridgean scheme did not? My answer must be: very little. The new evidence seems damaging; it is, however, not replacing. The new information assists our comprehension of lower level relationships but at higher levels it is too incomplete to provide the new construction that will substitute for the edifice it undermines. (2) What rearrangements of species and of putative relationships does it compel? If the data are accepted as implying the close relationship of the grahami and cristatellus groups, the alpha and beta dichotomy is indeed destroyed, although alpha and beta structure (and even groups) may perhaps still be usefully described. We then know that rebuilding is necessary without knowing how to do it. All relationships now have to be reassessed.

This in fact seems to me to be the take-home message. We need much new data - much more immunological data and much more data of every sort, and especially for the animals of Hispaniola, Cuba, and the mainland.

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The Third Anolis Newsletter reports two further years of the study of Anolis biology and also, as a new section, provides a list of the papers received by the Editor for the years 1973 through 1976. It is hoped to cite any papers missed for these years in a future number or numbers and to continue to record papers on Anolis biology. The Editor requests the assistance of all workers in the field in this regard.

Authors who send in their Anolis papers will receive the Newsletter free.

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